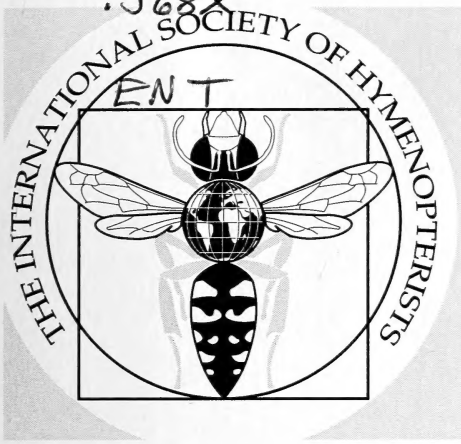


Journal of Hymenoptera Research

Volume 18, Number 2 **October 2009**

ISSN #1070-9428

DEDICATED TO THE MEMORY OF ROY SNELLING

CONTENTS

INTERNATIONAL SOCIETY OF HYMENOPTERISTS

Organized 1982; Incorporated 1991

All correspondence concerning Society business should be mailed to the appropriate officer at the following addresses: President, Plant Sciences Institute, Bldg. 003, Rm. 231 BARC-West, Beltsville, MD 20705, USA; Secretary, Department of Entomology, North Carolina State University, Campus Box 7613, 2301 Gardner Hall, Raleigh, NC 27695-7613, USA; Treasurer, Saint Louis University, 3507 LaClede Ave., St. Louis, MO 63103, USA; Editor, Dept. of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Membership. Members shall be persons who have demonstrated interest in the science of entomology. Annual dues for members are US$45.00 per year (US$40.00 if paid before 1 February), payable to The International Society of Hymenopterists. Requests for membership should be sent to the Treasurer (address above). Information on membership and other details of the Society may be found on the World Wide Web at http://hymenoptera.tamn.edu/ish/.

Journal. The *Journal of Hymenoptera Research* is published twice a year by the International Society of Hymenopterists, % Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0168, U.S.A. Members in good standing receive the *Journal*. Nonmember subscriptions are $60.00 (U.S. currency) per year.

The Society does not exchange its publications for those of other societies.

Please see inside back cover of this issue for information regarding preparation of manuscripts.

Statement of Ownership

Title of Publication: Journal of Hymenoptera Research.

Frequency of Issue: Twice a year.

Location of Office of Publication, Business Office of Publisher and Owner: International Society of Hymenopterists, 0 Department of Entomology, Smithsonian Institution, 10th and Constitution NW, Washington, D.C. 20560-0168, U.S.A.

Editor: Gavin R. Broad, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Managing Editor and Known Bondholders or other Security Holders: none.

This issue was mailed 2 October 2009

J. HYM. RES.
Vol. 18(2), 2009, pp. 123–124

EDITORIAL

Omnivorous Roy

"The turtle makes no progress until he sticks his head out."

"Arrogant? Anybody who has an opinion and expresses it in print is arrogant!"(Roy's response to being called arrogant)

Photograph courtesy of Kathy Horton

Roy R. Snelling, an outstanding figure in Hymenoptera research, died suddenly last year at the age of 73, while in the field in East Africa. Even as we regret that he did not have a great many more years, it was a most appropriate way to end a very good run.

Roy was legendarily opinionated, crusty, cantankerous ... and unfailingly generous to younger scientists who shared his passion for stinging insects. Even as he held no academic appointment, or even a university degree, many colleagues of a younger generation were effectively his students. The editors of this Festschrift are among those many.

He was an omnivore – taking the sensible view that his many and varied field trips required a flexible adaptation to the local diet – and a life-long enthusiast of all aculeates. His extensive published work was mostly in systematics and faunistics, with significant incursions into ecology and nesting biology.

Roy would have scoffed at the idea of a Festschrift in his memory. No matter. It is right and proper that those who admired him and benefited from his counsel should have an opportunity to demonstrate our esteem and affection. And – even as he continued to grumble – he would certainly have been gratified by this number of the *Journal of Hymenoptera Research*. The response to our call for contributions surpassed even our generous expectations, so that there are too many to fit into a single journal issue. The overflow is left for the succeeding issue.

In these pages you will find a biographical sketch and bibliography (Longino and G. Snelling), contributions from some of Roy's many research collaborators (e.g. Davidson et al.; Duffield et al.) and others from those who did not publish with him but have good reason to appreciate his guidance (e.g. Feener; Ward). Chew it well.

JUSTIN O. SCHMIDT & CHRISTOPHER K. STARR

(JOS) Southwestern Biological Institute, Tucson, AZ 85745, USA; email: ponerine@dakotacom.net
(CKS) Department of Life Sciences, University of the West Indies, St Augustine, Trinidad & Tobago; email: ckstarr@gmail.com

J. HYM. RES.
Vol. 18(2), 2009, pp. 125–135

An Inordinate Fondness for Things that Sting

JOHN T. LONGINO AND GORDON C. SNELLING

(JTL) Evergreen State College, Olympia, WA 98505, USA; email: longinoj@evergreen.edu
(GCS) 13161 Rancherias Road, Apple Valley, CA 92308, USA; email: myrmecophile@armyants.org

That so few now dare to be eccentric marks the chief danger of the time (John Stuart Mill)

This festschrift is in honor of an outstanding hymenopterist, Roy R. Snelling (1934–2008). Trager (2008) has provided a fine tribute to Roy's character and contributions. Roy was familiar to many of us not only for his publications but in his role as the keeper of the Hymenoptera collections at the Los Angeles County Museum of Natural History (LACM). In this introduction we give a brief biography and argue that this career so highly productive and important to generations of students could not readily happen in today's science.

Roy was born in 1934 in Turlock, California, USA, a small farming town in the heart of the San Joaquin Valley. In the 1930s Turlock was cited by *Ripley's Believe It or Not* as having the most churches per capita in the country. Since Roy was constitutionally froward, perhaps this explains his fervent atheism and vocal disapproval of religion. Somehow during those formative years in Turlock he developed an interest in insects. By the time he was 18 he was corresponding with J. C. Bequaert and R. M. Bohart and published his first paper, on mixed-species aggregations of *Polistes* queens.

His CV lists as his first job that of "Field Entomologist" with an agricultural company in Mexicali, Mexico, from 1953–1954. During this time his next four publications appear, and already he is showing both a solid focus on aculeates and a catholic approach within this group; two papers are on vespids, one is on a tiphiid, and the other is on an anthophorid. Around this time he attended a year and a half at Modesto Junior College, at which point he ended his formal higher education. One of the most notable hymenopterists of our time was self educated, without a college degree.

He underwent two years of military service from 1957–1959, at Fort Benning, Georgia. It is unclear whether he enlisted or was drafted, but he never spoke kindly of his time in Georgia. Even so, his time there was not entirely bereft of entomology; he later published a paper on a ripiphorid host from Georgia. He returned to California and obtained work in entomology as a Survey Entomologist and then Technician for the Bureau of Entomology, California Department of Agriculture. His time in the military and then with the California Department of Agriculture marked a five-year hiatus in his publication record. In 1962 he published another bee paper, around the time that he was offered two positions, one as a Curatorial Assistant at the LACM and a similar position at the Bernice P. Bishop Museum in Hawaii. The Bishop Museum job was considered more prestigious and was certainly in a more glamorous locale, but against his mentors' advice Roy chose the LACM. He preferred California for biotic and probably for cultural reasons. The rest of his career was at the LACM, where he consistently published taxonomy until his death in 2008, becoming a world authority on ants and bees.

Roy was married twice, with two sons and a daughter from his first marriage. His second wife, Ruth Ann DeNicola, participated in his scientific work by providing

Fig. 1. Roy in the ant aisle of the Los Angeles County Museum of Natural History, November 2008. Photo by J.T. Longino.

illustrations for a number of his publications, most notably his revision of *Myrmecocystus*. By the 1980's he was a bachelor again and remained so for the rest of his life. Roy is also survived by a brother. His son Gordon (one of the authors) also developed an interest in myrmecology, working on New World army ants and managing the myrmecology newsletter *Notes from Underground*.

Roy's mother was Cherokee. He deeply identified with his Native American heritage, which was a great source of pleasure and pride. He surrounded himself with early photos of Native Americans and numerous cultural emblems and liked to learn about indigenous groups wherever he traveled. He also incorporated indigenous names into many of the taxa he described, yielding such tongue-twisters to the anglocentric as *Myrmecocystus nequazcatl*, *Centris xochipillii*, and *Cephalotes kukulcan*. And he liked to look the part of an aboriginal son of the continent. Roy was an imposing man, often with a stern countenance, and he wore his hair in long braids. Many anecdotes revolve around first meetings, when the man who got off the plane or walked through the door caused jaws to drop and certainly did not match notions of what an ant taxonomist named Snelling would look like.

The dynamics at LACM were interesting. Roy began as a Curatorial Assistant, an entry-level civil service job, and remained at that level for 23 years. He became Collection Manager for his last six years before retirement. After retirement in 1993, right up until his death, he continued to work regularly at the museum. During his career at LACM he aggressively acquired collections, established an enviable publi-

cation record, and built an international reputation that helped put LACM entomology on the map. It is not clear whether his limited advancement at the museum was due to his lack of a PhD, personal choice, poor interactions with administrators, or some combination of these. He certainly had strong opinions and populist leanings. The security personnel and the cleaning staff all knew Roy and always exchanged friendly greetings, but relations with administrators were uniformly frosty. Still, administrations come and go, and Roy always outlasted them. Ultimately, Roy's choices must be seen as shrewd; by eschewing traditional notions of career advancement he was able to focus almost entirely on research, doing the work he loved.

Ants were not Roy's first love, and he only began paying attention to them as part of his work with the Department of Agriculture. His first ant publication was on the fire ants of the United States, motivated by the need to differentiate the imported fire ant from the native species. Even after this his work on ants was sparse for a long time, so that during the 1960s he published mostly on bees. It is clear, however, that his collecting and curating of ants was accelerating during this time. William Steel Creighton became an important mentor and colleague. When Creighton died in 1973, Roy arranged to acquire his collection for the LACM, as he would later do with the collections of William F. Buren and George & Jeanette Wheeler.

Roy's scientific publication list (see below) comprises 171 contributions. In these, he described 13 genus-group taxa and 20 species of bees, one genus and 78 species of ants, and one genus and four species-group taxa of social wasps, among others. His interests were eclectic, and he also published on Evaniidae, Tiphiidae, Eurytomidae, Pompilidae, Bethylidae, and even a behavioral note on a thomisid spider.

The "always question authority" attitude that is central to the scientific worldview was strong in Roy and extended to all aspects of his life. He despised fraud and sophistry and exposed it whenever possible. Chris Starr provided the following anecdote regarding one of Roy's favorite targets, Carlos Castaneda. Castaneda was an "anthropologist" who became famous in the late 1960s by describing training he supposedly received from a Yaqui shaman, Don Juan Matús. The Yaqui are a Native American people from the Sonoran region and a group with whom Roy was quite familiar. Even before Castaneda came generally to be regarded a fake (and Don Juan as a fictional character), Roy demonstrated this to his own satisfaction at one of Castaneda's public lectures. Rising in the question period, Roy asked "What is your name?" in Yaqui. Castaneda had no idea what he had said. Roy's reasoning: Castaneda cannot speak Yaqui; no Yaqui medicine man would stoop to speaking Spanish; therefore Castaneda had no way of communicating with Don Juan, and Don Juan did not exist. QED. For this and other reasons, Roy's conclusion is now generally accepted among anthropologists.

Roy was a natural historian, a collector, and an *identifier*. For many ecologists from the 1970s onward he was the "go to" guy for ant identifications. It is quite an irony that Roy, in so many ways a maverick, was also a great collaborator. He played particularly important roles in the work of Murray Blum and Tappey Jones (chemical ecology), Doyle McKey (ant-plant associations) and Dinah Davidson (ant community ecology, ant-plant associations). In an era when systematics was beginning to rise from the ashes, professional taxonomists began (and continue) to bristle at any hint of being "ecologists' handmaidens." This was a healthy development for systematics and one cannot denigrate systematists for focusing on revisionary work, but Roy's unique position allowed him to play a very important role. He encouraged countless young students of ants by being willing to identify samples that arrived in a hodge-

podge of screwcap vials, babyfood jars, and cardboard boxes, all filled with little bits of paper with pencil-scrawled code numbers from ecological studies. Where an average taxonomist would have responded very politely "Your work sounds really interesting; I really wish I could help you, but I just have so many other obligations right now...," Roy, after some harsh words for ecologists and their crummy samples, would say "Yeah, send 'em to me." On the other hand, he had no patience with medical doctors and others who thought he should identify their material gratis, even though they could well afford to pay.

One result of Roy's willingness to identify samples was that he greatly increased the strength and geographic coverage of the LACM ant collection. Another, perhaps more important, result was that he acted as a bridge between ecology and taxonomy. He introduced many ecologists to the importance and the techniques of taxonomy by turning their disorderly boxes of vials into ranks of properly mounted, labeled, and identified specimens in a leading museum collection. He opened their eyes to the wonderful diversity and form that underpinned their hypotheses. Students were sometimes chagrined to find that their "species A" was actually a genus with many species in the ecological community they were studying. Other times they were intrigued and fascinated by that diversity. Some even crossed the bridge that Roy formed, finding that there was an exciting sphere of academic activity and inquiry on the other side.

One of us (JTL) was one of those ecologists whose proclivities drew him across the bridge, leading to an extended period of work with Roy in the mid 1980s. LACM was awarded an NSF collections-improvement grant, primarily to integrate the Buren collection and Daniel H. Janzen's massive collection of Central America acacia ants. At the time, Longino was an under-employed tropical biologist based at

Fig. 2. Roy interacting with local kids on a collecting trip to Kenya, February 2000. Photographer unknown.

the University of California, Santa Barbara. He took a half-time position with the LACM for two years, commuting from Santa Barbara and working two (long) days a week in the museum. During that time he became intimately familiar with Roy's routine: 7 a.m., arrive, boil water in a scale-incrusted coffee pot, make execrable instant coffee, get to work; 10 a.m., coffee and a donut at the museum coffee shop downstairs (you could set your watch by the "Well, young fellah, time for a coffee break"); continue to feed the starlings donut crumbs and chat about museum politics, while the driven acolyte was eager to get back upstairs to work; after another period of work, lunch (Roy usually had something sausagey); 3 p.m., another coffee break; 4 p.m., depart for his Long Beach apartment. During this time Roy drove an MG. One of the more exhiliarating experiences was to drive with Roy to his apartment, screaming down LA freeways, inches above the pavement, open top, engine roaring, braids flying, darting through canyons of semi-truck trailers.

Roy's position at the LACM allowed a highly talented, self-educated taxonomist to make major contributions to science, to mentor and encourage students of nature, and to attract students to biological systematics. Roy was not compelled to turn his work space into a chemistry lab for DNA sequencing, to become the world expert on a single monophyletic taxon, or

to emphasize statistical analysis of macroecological patterns. He had the liberty to remain a generalized collector and identifier, and as a result was able to benefit a broad range of scientists. How many similar positions are available today?

ACKNOWLEDGMENTS

Jim Cane and Norm Johnson (Hymenoptera Name Server) helped with Roy's publication list. Justin Schmidt and Chris Starr were great sources and motivators.

LITERATURE CITED

Trager, J. 2008. Obituary: In memoriam – Roy R. Snelling (30 September 1934–21 April 2008). *Myrmecological News* 11: 227–229.

PUBLICATIONS OF ROY R. SNELLING

Snelling, R. 1952. Notes on nesting and hibernation of *Polistes* (Hymenoptera: Vespidae). *Pan-Pacific Entomologist* 28: 177.

Snelling, R. R. 1953. Notes on the nesting and hibernation of the wasp, *Mischocyttarus flavitarsis* (De Saussure) (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* 26: 143–145.

———. 1954. Wasps of the genus *Polistes* in California and Arizona (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* 27: 151–155.

———. 1954. The host of *Myrmosula rutilans* (Blake) (Hymenoptera: Tiphiidae). *Pan-Pacific Entomologist* 30: 124.

———. 1954. Records of *Exomalopsis sidae* in California and Baja California (Hymenoptera: Anthophoridae). *Pan-Pacific Entomologist* 30: 145.

———. 1955. Notes on some *Polistes* in the American Museum of Natural History, with descriptions of new North American subspecies (Hymenoptera, Vespidae). *American Museum Novitates* (1701): 1–9.

———. 1956. Bees of the genus *Centris* in California (Hymenoptera: Anthophoridae). *Pan-Pacific Entomologist* 32: 1–8.

———. 1962. Notes on the distribution of some southwestern megachilids, with descriptions of three new forms (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist* 38: 225–234.

———. 1963. The United States species of "fire ants" of the genus *Solenopsis*, subgenus *Solenopsis* Westwood, with synonymy of *Solenopsis aurea* Wheeler (Hymenoptera: Formicidae). *California Department of Agriculture, Bureau of Entomology, Occasional Papers* (3): 1–15.

———. 1963. The evaniid wasps of California (Hymenoptera: Evaniidae). *Pan-Pacific Entomologist* 39: 107–108.

———. 1963. A host of *Macrosaigon cruentum* (Germar) in Georgia (Coleoptera: Rhipiphoridae). *Pan-Pacific Entomologist* 39: 87–88.

———. 1965. Studies on California ants. 2. *Myrmecina californica* M. R. Smith (Hymenoptera; Formicidae). *Bulletin of the Southern California Academy of Sciences* 64: 101–105.

———. 1965. Studies on California ants. 1. *Leptothorax hirticornis* Emery, a new host and descriptions of the female and ergatoid male (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 64: 16–21.

———. 1966. The female of *Eucryptocerus placidus* (F. Smith) (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 65: 37–40.

———. 1966. Studies on North American bees of the genus *Hylaeus*, 1. Distribution of the western species of the subgenus *Prosopis* with descriptions of new forms (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (98): 1–13.

———. 1966. A new species of *Heteranthidium* from California (Hymenoptera: Megachilidae). *Contributions in Science, Natural History Museum of Los Angeles County* (97): 1–8.

———. 1966. Studies on North American bees of the genus *Hylaeus*, 2. Description of a new subgenus and species. *Proceedings of the Biological Society of Washington* 79: 139–144.

———. 1966. Studies on North American bees of the genus *Hylaeus*, 3. The Nearctic subgenera (Hymenoptera: Colletidae). *Bulletin of the Southern California Academy of Sciences* 65: 164–175.

———. 1966. The taxonomy and nomenclature of some North American bees of the genus *Centris* with descriptions of new species (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (112): 1–33.

———. 1967. Studies on California ants. 3. The taxonomic status of *Proceratium californicum* Cook (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (124): 1–10.

———. 1967. Description of a new subgenus of *Osmia* (Hymenoptera: Megachilidae). *Bulletin of the Southern California Academy of Sciences* 66: 103–108.

Creighton, W. S. and R. R. Snelling. 1967 ("1966"). The rediscovery of *Camponotus* (*Myrmaphaenus*) *yogi* Wheeler (Hymenoptera: Formicidae). *Psyche* 73: 187–195.

Snelling, R. R. 1968. Honey ants, the industrious socialites. *Museum Alliance Quarterly* 7: 14–18.

———. 1968. A new species of *Eurhopalothrix* from El Salvador (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (154): 1–4.

———. 1968. Taxonomic notes on some Mexican cephalotine ants (Hymenoptera: Formicidae).

Contributions in Science, Natural History Museum of Los Angeles County (132): 1–10.

———. 1968. Studies on California ants. 4. Two species of *Camponotus* (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 70: 350–358.

———. 1968. Studies on North American bees of the genus *Hylaeus*. 4. The subgenera *Cephalylaeus*, *Metziella* and *Hylaeana* (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (144): 1–6.

———. 1969. Notes on the systematics and dulosis of some western species of *Formica*, subgenus *Raptiformica* (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 71: 194–197.

———. 1969. The repository of the T. W. Cook ant types (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 68: 57–58.

———. 1969. Taxonomic notes on the *Myrmecocystus melliger* complex (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (170): 1–9.

———. 1969. The Philippine subgenus *Hoploprosopis* of *Hylaeus* (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (171): 1–5.

———. 1970. Studies on California ants, 5. Revisionary notes on some species of *Camponotus*, subgenus *Tanaemyrmex* (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 72: 390–397.

———. 1970. Studies of North America bees of the genus *Hylaeus*. 5. The subgenus *Hylaeus*, *s. str.* and *Paraprosopis* (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (180): 1–59.

———. 1970. Ant warfare - offensive and defensive maneuvers. *Museum Alliance Quarterly* 8: 10–15.

———. 1970. The *Hylaeus* of the Bonin Islands, western Pacific Ocean (Hymenoptera: Colletidae). *Bulletin of the Southern California Academy of Sciences* 69: 1–19.

———. 1970. The social wasps of Lower California, Mexico (Hymenoptera: Vespidae). *Contributions in Science, Natural History Museum of Los Angeles County* (197): 1–20.

———. 1971. A new species of *Simopelta* from Costa Rica (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 70: 16–17.

———. 1971. Studies on California ants. 6. Three new species of *Myrmecocystus* (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (214): 1–16.

Blum, M. S., J. M. Brand, R. M. Duffield, and R. R. Snelling. 1973. Chemistry of the venom of *Solenopsis aurea* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 66: 702.

Snelling, R. R. 1973. Studies on California ants. 7. The genus *Stenamma* (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (245): 1–38.

———. 1973. Two ant genera new to the United States (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (236): 1–8.

———. 1973. The ant genus *Conomyrma* in the United States (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (238): 1–6.

Creighton, W. S. and R. R. Snelling. 1974. Notes on the behavior of three species of *Cardiocondyla* in the United States (Hymenoptera: Formicidae). *Journal of the New York Entomological Society* 82: 82–92.

Snelling, R. R. 1974. High rise in the ant world. *Terra* 12: 15–17.

———. 1974. Studies on California ants. 8. A new species of *Cardiocondyla* (Hymenoptera: Formicidae). *Journal of the New York Entomological Society* 82: 76–81.

———. 1974. Changes in the status of some North American *Polistes* (Hymenoptera: Vespidae). *Proceedings of the Entomological Society of Washington* 76: 476–479.

———. 1974. Notes on the distribution and taxonomy of some North American *Centris* (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (259): 1–41.

Hunt, J. H. and R. R. Snelling. 1975. A checklist of the ants of Arizona. *Journal of the Arizona Academy of Science* 10: 20–23.

Snelling, R. R. 1975. Descriptions of new Chilean ant taxa (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (274): 1–19.

———. 1975. A new North American genus of Eumenidae (Hymenoptera: Vespoidea). *Proceedings of the Entomological Society of Washington* 77: 56–58.

———. 1975. Taxonomic notes on some colletid bees of western North America with descriptions of new species (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (267): 1–9.

———. 1975. Range extension of two *Heteranthidium*, with description of *H. cordaticeps* male (Hymenoptera: Megachilidae). *Proceedings of the Entomological Society of Washington* 77: 87–90.

——— and J. H. Hunt. 1975. The ants of Chile (Hymenoptera: Formicidae). *Revista Chilena de Entomología* 9: 63–129.

——— and A. S. Menke. 1975. *Vespula germanica* (Fabricius), an adventive yellowjacket in the northeastern United States (Hymenoptera: Vespidae). *Cooperative Economic Insect Report, U. S. Department of Agriculture* 25: 193–200.

———. 1976. A revision of the honey ants, genus *Myrmecocystus* (Hymenoptera: Formicidae). *Natural History Museum Los Angeles County Science Bulletin* 24: 1–163.

Francoeur, A. and R. R. Snelling. 1979. Notes for a revision of the ant genus *Formica*. 2. Reidentifications for some specimens from the T. W. Cook collection and new distribution data (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (309): 1–7.

Snelling, R. R. 1979. Three new species of the Palaeotropical arboreal ant genus *Cataulacus* (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (315): 1–8.

———. 1979. *Aphomomyrmex* and a related new genus of arboreal African ants (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (316): 1–8.

——— and C. D. George. 1979. The taxonomy, distribution and ecology of California desert ants. *Report to California Desert Plan Program, Bureau of Land Management, U.S. Dept. Interior*. 335 + 89 pp.

Duffield, R. M., A. Fernandes, S. McKay, J. W. Wheeler, and R. R. Snelling. 1980. Chemistry of the exocrine secretions of *Hylaeus modestus* (Hymenoptera: Colletidae). *Comparative Biochemistry and Physiology* 67B: 159–162.

Snelling, R. R. 1980. New bees of the genus *Hylaeus* from Sri Lanka and India (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (328): 1–18.

———. 1980. The bee genus *Bicornelia* (Hymenoptera: Colletidae). *Contributions in Science, Natural History Museum of Los Angeles County* (327): 1–6.

———. 1981. Systematics of social Hymenoptera. Pp. 369–453 *in* H. R. Hermann, ed. *Social insects. Volume 2*. Academic Press, New York. xiii+491 p.

Blum, M. S., T. H. Jones, R. R. Snelling, W. L. Overal, H. M. Fales, and R. J. Highet. 1982. Systematic implications of the exocrine chemistry of some *Hypoclinea* species. *Biochemical Systematics and Ecology* 10: 91–94.

Snelling, R. R. 1982 ("1981"). The taxonomy and distribution of some North American *Pogonomyrmex* and descriptions of two new species (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 80: 97–112.

———. 1982. The taxonomy of some neotropical *Hylaeus* and descriptions of new taxa. *Bulletin of the Southern California Academy of Sciences* 81: 1–25.

———. 1982. A revision of the honey ants, genus *Myrmecocystus*, first supplement (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 81: 69–86.

———. 1983. Prey-stalking behavior of a thomisid spider, *Xysticus californicus* Keyserling (Araneae: Thomisidae). *Entomological News* 94: 201–203.

———. 1983. Taxonomic and nomenclaturial studies on American polistine wasps (Hymenoptera: Vespidae). *Pan-Pacific Entomologist* 59: 267–280.

———. 1983. The North American species of the bee genus *Lithurge* (Hymenoptera: Megachilidae). *Contributions in Science, Natural History Museum of Los Angeles County* (343): 1–11.

———. 1983. Studies on North American bees of the genus *Hylaeus*: 6. An adventive Palearctic species in Southern California (Hymenoptera: Colletidae). *Bulletin of the Southern California Academy of Sciences* 82: 12–16.

———. 1984. Studies on the taxonomy and distribution of American centridine bees (Hymenotpera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (347): 1–69.

———. 1984. Notes on distribution of evaniid wasps in western North America (Hymenoptera: Evaniidae). *Entomological News* 95: 27–28.

——— and T. J. Zavortink. 1984. A revision of the cleptoparasitic bee genus *Ericrocis* (Hymenoptera: Anthophoridae). *Wasmann Journal of Biology* 42: 1–26.

Blum, M. S., T. H. Jones, H. A. Lloyd, H. M. Fales, R. R. Snelling, Y. Lubin, and J. Torres. 1985. Poison gland products of *Solenopsis* and *Monomorium* species. *Journal of Entomological Science* 20: 254–257.

Snelling, R. R. 1985. [Untitled. *Camponotus bakeri* Wheeler 1904 (elevated from subspecies of *C. hyatti*).], p. 24, *in* Miller, S.E., The California Channel Islands – past, present and future: an entomological perspective. Pp. 3–28 *in* Menke, A. S. and D. R. Miller, eds. *Entomology of the California Channel Islands. Proceedings of the first symposium*. Santa Barbara Museum of Natural History, Santa Barbara.

———. 1985. The systematics of the hylaeine bees (Hymenoptera: Colletidae) of the Ethiopian zoologeographical region: The genera and subgenera with revisions of the smaller groups. *Contributions in Science, Natural History Museum of Los Angeles County* (361): 1–33.

——— and R. W. Brooks. 1985. A review of the genera of cleptoparasitic bees of the tribe Ericrocini (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (369): 1–34.

——— and W. F. Buren. 1985. Description of a new species of slave-making ant in the *Formica sanguinea* group (Hymenoptera: Formicidae). *Great Lakes Entomologist* 18: 69–78.

Rozen, J. G., Jr and R. R. Snelling. 1986. Ethology of the bee *Exomalopsis nitens* and its cleptoparasite (Hymenoptera: Anthophoridae). *Journal of the New York Entomological Society* 94: 480–488.

Ruttner, F., E. C. Wilson, R. Snelling, G. Vorwohl, and D. Kauhausen. 1986. Die Evolution des Flügelgeaders der Honigbienen. *Apidologie* 17: 348–350.

Schmidt, J. O., P. J. Schmidt, and R. R. Snelling. 1986. *Pogonomyrmex occidentalis*, an addition to the ant fauna of Mexico, with notes on other species of harvester ants from Mexico (Hymenoptera: Formicidae). *Southwestern Naturalist* 31: 395–396.

Snelling, R. R. 1986. New synonymy in Caribbean ants of the genus *Leptothorax* (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 88: 154–156.

———. 1986. Contributions toward a revision of the new world nomadine bees. A partitioning of the genus *Nomada* (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (376): 1–32.

———. 1986. The taxonomic status of two North American *Lithurge*, Hymenoptera: Megachilidae. *Bulletin of the Southern California Academy of Sciences* 85: 29–34.

———. 1986. The taxonomy and nomenclature of some Australian paragiine wasps (Hymenoptera: Masaridae). *Contributions in Science, Natural History Museum of Los Angeles County* (378): 1–19.

Stage, G. I. and R. R. Snelling. 1986. The subfamilies of Eurytomidae and systematics of the subfamily Heimbrinae (Hymenoptera: Chalcidoidea). *Contributions in Science, Natural History Museum of Los Angeles County* (375): 1–17.

Snelling, R. R. 1987. A revision of the bee genus *Aztecanthidium* (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist* 63: 165–171.

——— and in Rozen, J. G., Jr. 1987. [Description of *Hesperapis* (*Hesperapis*) *trochanterata*, new species] Nesting biology and immature stages of a new species in the bee genus *Hesperapis* (Hymenoptera: Apoidea: Melittidae: Dasypodinae). *American Museum Novitates* (2887): 1–13.

——— and J. G. Rozen, Jr 1987. Contributions toward a revision of the New World nomadine bees. 2. The genus *Melanomada* (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* (384): 1–12.

Blum, M. S., R. R. Snelling, R. M. Duffield, H. R. Hermann, and H. A. Lloyd. 1988. Mandibular gland chemistry of *Camponotus* (*Myrmothrix*) *abdominalis*: chemistry and chemosystematic implications (Hymenoptera: Formicidae). Pp. 481–490 *in* J. C. Trager ed. *Advances in Myrmecology*. E. J. Brill, Leiden, xxvii + 551 p.

Davidson, D. W., J. T. Longino, and R. R. Snelling. 1988. Pruning of host plant neighbors by ants: an experimental approach. *Ecology* 69: 801–808.

Duffield, R. M., J. W. Wheeler, and R. R. Snelling. 1988. Mellein in the mandibular glands of worker *Camponotus ferrugineus* (Fabr.): an anomoly [sic] in the subgenus *Camponotus*. Pp. 475–480 *in* J. C. Trager ed. *Advances in Myrmecology*. E. J. Brill, Leiden. xxvii + 551 p.

Snelling, R. R. 1988. Taxonomic notes on Nearctic species of *Camponotus*, subgenus *Myrmentoma* (Hymenoptera: Formicidae). Pp. 55–78 *in* J. C. Trager, ed. *Advances in Myrmecology*. E. J. Brill, Leiden. xxvii + 551 p.

———. 1988. Geographical inexactitude. *Pan-Pacific Entomologist* 63: 339–340.

———. 1988. The generic placement of *Prosopis*? *Allodape*? *mustela* Vachal, 1895 (Hymenoptera: Apoidea). *Entomological News* 99: 10–12.

———. 1988. A new species of *Centris* (Melanocentris) from Cerro de la Neblina, Venezuela (Hymenoptera: Anthophoridae). *Entomological News* 99: 13–16.

Davidson, D. W., R. R. Snelling, and J. T. Longino. 1989. Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21: 64–73.

Lloyd, H. A., M. S. Blum, R. R. Snelling, and S. L. Evans. 1989. Chemistry of mandibular and Dufour's gland secretions of ants in genus *Myrmecocystus*. *Journal of Chemical Ecology* 15: 2589–2599.

Snelling, R. R. 1990. A review of the native North American bees of the genus *Chalicodoma* (Hymenoptera: Megachilidae). *Contributions in Science, Natural History Museum of Los Angeles County* 421: 1–39.

Davidson, D. W., R. B. Foster, R. R. Snelling, and P. W. Lozada. 1991. Variable composition of some tropical ant-plant symbioses. Pp. 145–162 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson eds. *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley, New York, xiv + 639 p.

Snelling, R. R. 1992. Two unusual new myrmicine ants from Cameroon (Hymenoptera: Formicidae). *Psyche* 99: 95–101.

———. 1992. A newly adventive ant of the genus *Pheidole* in southern California (Hymenoptera: Formicidae). *Bulletin of the Southern California Academy of Sciences* 91: 121–125.

———. 1992. A new species of the bee genus *Anthidium* (Hymenoptera: Megachilidae) from western North America. *Entomological News* 103: 175–179.

——— and S. P. Cover. 1992. Description of a new *Proceratium* from Mexico (Hymenoptera: Formicidae). *Psyche* 99: 49–53.

——— and B. N. Danforth. 1992. A review of *Perdita*, subgenus *Macrotera* (Hymenoptera: Andrenidae). *Contributions in Science, Natural History Museum of Los Angeles County* (436): 1–12.

——— and J. T. Longino. 1992. Revisionary notes on the fungus-growing ants of the genus *Cyphomyrmex*, *rimosus* group (Hymenoptera: Formicidae: Attini). Pp. 479–494 *in* D. Quintero and A. Aiello,

eds. *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, Oxford. xxii + 692 p.

Blum, M. S., T. M. M. Ali, T. H. Jones, and R. R. Snelling. 1994. Identification of a chemical releaser of alarm behavior for workers of *Harpegnathos saltator* Jerd. (Hymenoptera, Formicidae). *Memorabilia Zoologica* 48: 17–22.

Snelling, R. R. 1994. *Diadasia*, subgenus *Disiapis*, in North America (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* 448: 1–8.

Dejean, A., I. Olmstead, and R. R. Snelling. 1995. Tree-epiphyte-ant relationships in the low inundated forest of Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. *Biotropica* 27: 57–70.

Perfecto, I. and R. R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications* 5: 1084–1097.

Snelling, R. R. 1995. Systematics of Nearctic ants of the genus *Dorymyrmex* (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (454): 1–14.

———. 1995 ("1992"). A new spider wasp of the genus *Psorthaspis* from the Greater Antilles (Hymenoptera: Pompilidae; Pompilinae). *Acta Científica* 6: 103–108.

——— and G. I. Stage. 1995. Systematics and biology of the bee genus *Xeralictus* (Hymenoptera: Halictidae, Rophitinae). *Contributions in Science, Natural History Museum of Los Angeles County* (451): 1–17.

——— and G. I. Stage. 1995. A revision of the nearctic Melittidae: the subfamily Melittinae. *Contributions in Science, Natural History Museum of Los Angeles County* (451): 19–31.

Torres, J. A. and R. R. Snelling. 1995 ("1992"). Los himenópteros de Isla de Mona. *Acta Científica* 6: 87–102.

Jones, T. H., J. A. Torres, R. R. Snelling, and T. F. Spande. 1996. Primary tetradecenyl amines from the ant *Monomorium floricola*. *Journal of Natural Products* 59: 801–802.

———, J. A. Torres, T. F. Spande, H. M. Garraffo, M. S. Blum, and R. R. Snelling. 1996. Chemistry of venom alkaloids in some *Solenopsis* (*Diplorhoptrum*) species from Puerto Rico. *Journal of Chemical Ecology* 22: 1221–1236.

Snelling, R. R. 1996. Systematic notes on some Bethylidae from the Virgin Islands and Puerto Rico (Hymenoptera: Chrysidoidea). *Memoirs of the Entomological Society of Washington* 17: 194–208.

Cane, J. H., R. R. Snelling, L. J. Kervin, and G. C. Eickwort. 1997. A new monolectic coastal bee, *Hesperapis oraria* Snelling and Stage (Hymenoptera: Melittidae), with a review of desert and neotropical disjunctives in the southeastern U.S. *Journal of the Kansas Entomological Society* 69 (Suppl.): 238–247.

Dejean, A., B. Corbara, R. R. Snelling, and M. Belin-Depoux. 1997. Les jardins de fourmis de Guyane Française: Relations entre arbres support, epiphytes et fourmis. *Acta Botanica Gallica* 144: 333–345.

Snelling, R. R. 1997. *Polistes tepidus malayanus* Cameron erroneously reported from the Hawaiian Islands (Hymenoptera: Vespidae). *Records of the Hawaii Biological Survey for 1997* 56: 33–35.

Torres, J. A. and R. R. Snelling. 1997. Biogeography of Puerto Rican ants: a non-equilibrium case? *Biodiversity and Conservation* 6: 1103–1121.

Frankie, G. W., S. B. Vinson, M. A. Rizzardi, T. L. Griswold, S. O'Keefe, and R. R. Snelling. 1998. Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. *Journal of the Kansas Entomological Society* 70: 281–296.

Gorman, J. S. T., T. H. Jones, T. F. Spande, R. R. Snelling, J. A. Torres, and H. M. Garraffo. 1998. 3-hexyl-5-methylindolizidine isomers from thief ants, *Solenopsis* (*Diplorhoptrum*) species. *Journal of Chemical Ecology* 24: 933–943.

Snelling, R. R. 1998. Social Hymenoptera of the Lakekamu Basin. Pp. 39–46, 131–146 *in* Mack, A. L. ed. *A Biological Assessment of the Lakekamu Basin Papua New Guinea*. Conservation International, Washington D.C. 187 pp.

——— and J. A. Torres. 1998. *Camponotus ustus* Forel and two similar new species from Puerto Rico (Hymenoptera: Formicidae). *Contributions in Science, Natural History Museum of Los Angeles County* (469): 1–10.

Jones, T. H., R. C. Flournoy, J. A. Torres, R. R. Snelling, T. F. Spande, and H. M. Garraffo. 1999. 3-methyl-4-phenylpyrrole from the ants *Anochetus kempfi* and *Anochetus mayri*. *Journal of Natural Products* 62: 1343–1345.

———, J. S. T. Gorman, R. R. Snelling, J. H. C. Delabie, M. S. Blum, H. M. Garraffo, P. Jain, J. W. Daly, and T. F. Spande. 1999. Further alkaloids common to ants and frogs: decahydroquinolines and a quinolizidine. *Journal of Chemical Ecology* 25: 1179–1193.

———, T. J. Wojciechowski, R. R. Snelling, J. A. Torres, P. Chacon, and P. J. DeVreis. 1999. Dialkylpyrrolidines from the ants *Megalomyrmex cyendyra* Brandao and *M. latreillei* Emery. *Caribbean Journal of Science* 35: 310–311.

Snelling, R. R. 1999. [Untitled. *Cephalotes kukulcan* Snelling new species.]. Pp. 402–410 *in* de Andrade, M. L. and C. Baroni-Urbani eds. *Diversity and Adaptation in the Ant Genus Cephalotes Past and Present. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 271: 1–889.

———. 1999. [Untitled. *Cephalotes chacmul* Snelling new species.]. Pp. 611–615 *in* de Andrade, M. L. and C. Baroni-Urbani eds. *Diversity and Adaptation in the Ant Genus Cephalotes Past and Present.*

Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 271: 1–889.

Spande, T. F., P. Jain, H. M. Garraffo, L. K. Pannell, H. J. C. Yeh, J. W. Daly, S. Fukumoto, K. Imamura, T. Tokuyama, J. A. Torres, R. R. Snelling, and T. H. Jones. 1999. Occurrence and significance of decahydroquinolines from dendrobatid poison frogs and a myrmicine ant: use of 1H and 13C NMR in their conformational analysis. *Journal of Natural Products* 62: 5–21.

Daly, J. W., H. M. Garraffo, P. Jain, T. F. Spande, R. R. Snelling, C. Jaramillo, and A. S. Rand. 2000. Arthropod-frog connection: Decahydroquinoline and pyrrolizidine alkaloids common to microsympatric myrmicine ants and dendrobatid frogs. *Journal of Chemical Ecology* 26: 73–85.

Dejean, A., B. Corbara, J. Orivel, R. R. Snelling, J. H. C. Delabie, and M. Belin-Depoux. 2000. The importance of ant gardens in the pioneer vegetal formations of French Guiana (Hymenoptera: Formicidae). *Sociobiology* 35: 425–439.

Snelling, R. R. 2000. A review of the *Camponotus montivagus* complex (Hymenoptera: Formicidae). *Sociobiology* 36: 599–611.

———. 2000. Ants of the Wapoga River area, Irian Jaya, Indonesia. Pages 43–46, 96–100 *in RAP Bulletin of Biological Assessment* (Conservation International), #14.

Torres, J. A., R. R. Snelling, and M. Canals. 2000. New records of parasitoids of Aculeate Hymenoptera in Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* 84: 99–100.

———, R. R. Snelling, and T. H. Jones. 2000. Distribution, ecology and behavior of *Anochetus kempfi* (Hymenoptera: Formicidae) and description of the sexual forms. *Sociobiology* 36: 505–516.

Garraffo, H. M., T. F. Spande, P. Jain, T. Kaneko, T. H. Jones, M. S. Blum, T. M. M. Ali, R. R. Snelling, L. A. Isbell, H. G. Robertson, and J. W. Daly. 2001. Ammonia chemical ionization tandem mass spectrometry in structural determination of alkaloids. II. Tetraponerines from pseudomyrmecine ants. *Rapid Communications in Mass Spectrometry* 15: 1409–1415.

Snelling, R. R. 2001. Two new species of thief ants (*Solenopsis*) from Puerto Rico (Hymenoptera: Formicidae). *Sociobiology* 37: 511–525.

Torres, J. A., R. R. Snelling, M. S. Blum, R. C. Flournoy, T. H. Jones, and R. M. Duffield. 2001. Mandibular gland chemistry of four Caribbean species of *Camponotus* (Hymenoptera : Formicidae). *Biochemical Systematics and Ecology* 29: 673–680.

———, R. R. Snelling, and M. Canals. 2001. Seasonal and nocturnal periodicities in ant nuptial flights in the tropics (Hymenoptera: Formicidae). *Sociobiology* 37: 601–626.

———, V. E. Zottig, J. E. Co, T. H. Jones, and R. R. Snelling. 2001. Caste specific alkaloid chemistry of *Solenopsis maboya* and *S-torresi* (Hymenoptera : Formicidae). *Sociobiology* 37: 579–583.

Duffield, R. M. and R. R. Snelling. 2002. *Tapinoma sessile* (Say) (Hymenoptera : Formicidae) nest in association with the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae). *Proceedings of the Entomological Society of Washington* 104: 814–816.

Durou, S., A. Dejean, I. Olmsted, and R. R. Snelling. 2002. Ant diversity in coastal zones of Quintana Roo, Mexico, with special reference to army ants. *Sociobiology* 40: 385–402.

Longino, J. T. and R. R. Snelling. 2002. A taxonomic revision of the *Procryptocerus* (Hymenoptera: Formicidae) of Central America. *Contributions in Science, Natural History Museum of Los Angeles County* (495): 1–30.

Co, J. E., T. H. Jones, A. Hefetz, A. Tinaut, and R. R. Snelling. 2003. The comparative exocrine chemistry of nine Old World species of *Messor* (Formicidae : Myrmicinae). *Biochemical Systematics and Ecology* 31: 367–373.

Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300: 969–972.

Dejean, A., S. Durou, I. Olmsted, R. R. Snelling, and J. Orivel. 2003. Nest site selection by ants in a flooded Mexican mangrove, with special reference to the epiphytic orchid *Myrmecophila christinae*. *Journal of Tropical Ecology* 19: 325–331.

Jones, T. H., D. A. Clark, B. E. Heterick, and R. R. Snelling. 2003. Farnesylamine from the ant *Monomorium fieldi* Forel. *Journal of Natural Products* 66: 325–326.

———, V. E. Zottig, H. G. Robertson, and R. R. Snelling. 2003. The venom alkaloids from some African *Monomorium* species. *Journal of Chemical Ecology* 29: 2721–2727.

Snelling, R. R. 2003. Bees of the Hawaiian Islands, exclusive of *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 76: 342–356.

Davidson, D. W., S. C. Cook, and R. R. Snelling. 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. *Oecologia* 139: 255–266.

Jones, T. H., D. A. Clark, A. A. Edwards, D. W. Davidson, T. F. Spande, and R. R. Snelling. 2004. The chemistry of exploding ants, *Camponotus* spp. (*cylindricus* complex). *Journal of Chemical Ecology* 30: 1479–1492.

Snelling, R. R. and J. A. Torres. 2004. The spider wasps of Puerto Rico and the British Virgin Islands (Hymenoptera: Pompilidae). *Journal of the Kansas Entomological Society* 77: 356–376.

Davidson, D. W., S. C. Cook, and R. R. Snelling. 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications.

Oecologia 139: 255–266 (Erratum: Oecologia 143: 335).

Jones, T. H., S. R. Brunner, A. A. Edwards, D. W. Davidson, and R. R. Snelling. 2005. 6-alkylsalicylic acids and 6-alkylresorcylic acids from ants in the genus *Crematogaster* from Brunei. *Journal of Chemical Ecology* 31: 407–417.

Snelling, R. R. 2005. Wasps, ants, and bees: Aculeate Hymenoptera. Pp. 283–296 *in* and J. Lazell. *Island: Facts and Theory in Nature*. University of California Press, Berkeley. 382 p.

———. 2006. Taxonomy of the *Camponotus festinatus* complex in the United States of America (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 8: 83–97.

Wetterer, J. K. and R. R. Snelling. 2006. The red imported fire ant, *Solenopsis invicta*, in the Virgin Islands (Hymenoptera : Formicidae). *Florida Entomologist* 89: 431–434.

Jones, T. H., H. L. Voegtle, H. M. Miras, R. G. Weatherford, T. F. Spande, H. M. Garraffo, J. W. Daly, D. W. Davidson, and R. R. Snelling. 2007. Venom chemistry of the ant *Myrmicaria melanogaster* from Brunei. *Journal of Natural Products* 70: 160–168.

Snelling, G. C. and R. R. Snelling. 2007. New synonymy, new species, new keys to *Neivamyrmex* army ants of the United States. Pp. 459–550 *in* Snelling, R. R., B. L. Fisher and P. S. Ward eds. *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson - 50 years of Contributions. Memoirs of the American Entomological Institute* 80.

Snelling, R. R. 2007. Preface. Pp. 1–2 *in* Snelling, R. R., B. L. Fisher and P. S. Ward eds. *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson - 50 years of Contributions. Memoirs of the American Entomological Institute* 80.

———. 2007. A review of the arboreal Afrotropical ant genus *Axinidris*. Pp. 551–579 *in* Snelling, R. R., B. L. Fisher and P. S. Ward, eds. *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson - 50 years of Contributions. Memoirs of the American Entomological Institute* 80.

Snelling, R. R., B. L. Fisher and P. S. Ward, eds. 2007 *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson - 50 years of Contributions. Memoirs of the American Entomological Institute* 80.

Snelling, R. R. 2008. A new name for *Myopias punctigera* (Emery 1901), not *M-maligna* var. *punctigera* (Emery 1900) (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 110: 261–261.

Voegtle, H. L., T. H. Jones, D. W. Davidson, and R. R. Snelling. 2008. E-2-ethylhexenal, E-2-ethyl-2-hexenol, mellein, and 4-hydroxymellein in *Camponotus* species from Brunei. *Journal of Chemical Ecology* 34: 215–219.

Duffield, R. M., R. R. Snelling, H. M. Fales, and M. S. Blum. 2009. Mandibular gland chemistry of two Nearctic species of *Camponotus (Colobopsis)* (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* 18: 140–144.

Snyder, A. J., T. H. Jones, G. C. Snelling, and R. R. Snelling. 2009. Venom alkaloids from some *Monomorium* species. *Journal of Hymenoptera Research* 18: 145–150.

Snelling, R. R., G. C. Snelling, J. O. Schmidt, and S. P. Cover. 2009. The sexual castes of *Pogonomyrmex anzensis* Cole (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* 18: 315–321.

J. HYM. RES.
Vol. 18(2), 2009, pp. 136–139

Interspecific Adoption of Orphaned Nests by *Polistes* Paper Wasps (Hymenoptera: Vespidae)

JAMES H. HUNT

Departments of Biology and Entomology and W. M. Keck Center for Behavioral Biology, North Carolina State University, Campus Box 7613, Raleigh, NC 27695; email: jim_hunt@ncsu.edu

Abstract.—Two occurrences are described in which a *Polistes* paper wasp of one species took up residence on a nest built by and containing the brood of a different *Polistes* species. These observations are placed in the context of previous reports of shared nesting, intraspecific and interspecific nest usurpation, and intraspecific and interspecific adoption of orphaned nests. These observations suggest a scenario for the possible origin of social parasitism in *Polistes*.

Roy Snelling's first publication (Snelling 1952) reports observations that apparently were made in the nesting season of 1950 and in non-nesting seasons that could have been even earlier. His short note is given here in its entirety.

NOTES ON NESTING AND HIBERNATION OF POLISTES

(Hymenoptera: Vespidae)
Robert [sic] Snelling
Turlock, California

Students have known for some time that occasionally two females (queens) of *Polistes* will found a nest together. Those recorded were noted to be of the same species. However, on one occasion I have taken a female each of *Polistes fuscatus aurifer* Saussure[1] and *P. apachus* Saussure contributing toward a future colony together. As they were watched for some time there is very little chance of an error. In a letter of January 30, 1951, J. C. Bequaert comments that, "Whether queens of different species could be successful in this is not known." Unfortunately, I collected the wasps and nest at once. At the time, there were thirteen cells with larvae and eggs.

In hibernation, the social Vespidae are rather gregarious. At various times I have taken *P. f. aurifer, P. apachus, P. hunteri californicus* Bohart, *Vespula pennsylvanica* Saussure, and *Mischocyttarus flavitarsis* Saussure hibernating together. In fact, I have taken three of *aurifer*, seven of *P. h. californicus*, two of *M. flavitarsis* and a few inches away, several of *V. pennsylvanica*.

[1]The wasps were identified by Dr. R. M. Bohart. I am indebted to him and to Dr. J. C. Bequaert for help.

Multi-species wintering aggregations of *Polistes* had been previously reported (e.g. Rau and Rau 1918, p. 285), but Snelling's observation of shared nesting between two *Polistes* species may have been the first of its kind. Two publications subsequent to Snelling (1952) report similar observations. Hunt and Gamboa (1978) reported shared nesting between *Polistes metricus* Say and *P. fuscatus* (Fabricius). In one case, in Missouri, a single *P. metricus* shared a nest with two *P. fuscatus*. Numerous *P. fuscatus* but no *P. metricus* were reared from the nest. In another case, in Kansas, two *P. metricus* were apparently dominant to a *P. fuscatus* on a nest that was subsequently lost to parasitoids. O'Donnell and Jeanne (1991) reported a case from Costa Rica in which a single *P. canadensis* (L.) was behaviorally dominant over three *P. instabilis* Saussure that had apparently initiated the nest. In time, the *P. instabilis* females

disappeared from the nest, and other *P. canadensis* females joined the colony. Only *P. canadensis* brood was identified in the nest.

In the Missouri case, the nest had been initiated by a single foundress of a third species, either *Polistes carolina* (L.) or *Polistes perplexus* Cresson. These two species are distinctive by virtue of their red color and are easily recognized among the Missouri paper wasp fauna, yet they can be distinguished from one another only by close examination. Both have been recorded at the study site. I had moved the nest from its initial location to a window observation box, and the foundress was present 1 and 3 days following the transfer, but she abandoned the nest thereafter. The two other species were together on the nest when it was checked 10 days later. Thus the shared nesting was also a case of interspecific adoption of an orphan nest. Here I report two additional observations of interspecific nest adoption in *Polistes*.

RESULTS

Daily monitoring of a population of *Polistes metricus* in nest boxes at Washington University's Tyson Research Station near St. Louis, Missouri, revealed a colony in which the single foundress was last seen on 3 June, 2005. Five pupae plus nine larvae of various instars remained in the untended 14-cell nest until 15 June, 2005. On that date a single female *Polistes carolina* or *Polistes perplexus* was found to be present on the nest. The *P. metricus* brood was intact and had not been cannibalized. The red *Polistes* was standing on the face of the nest in a posture characteristic of foundresses. The *P. metricus* pupal brood was due for experimental collection on that date (Hunt et al. 2007), and the red *Polistes* escaped collection. The nest, with larvae still present, could have been replaced, but it was not, thus it cannot be known if this incipient interspecific adoption of an orphan nest might have been successful.

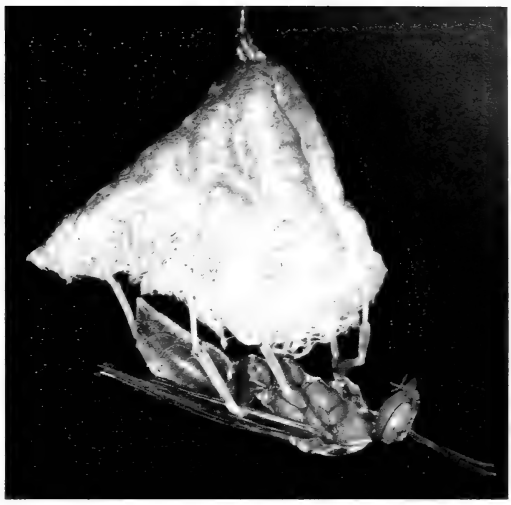


Fig. 1. A female *Polistes metricus* on a nest constructed by *Polistes exclamans*. Photo taken on 26 June 2008 by Freddie-Jeanne Richard.

On 21 May 2008, a nest of *Polistes exclamans* Viereck in a nest box at North Carolina State University's Lake Wheeler Honey Bee Research Facility near Raleigh, NC, was recorded to have a single foundress with eighteen larvae and three eggs in its 21-cell nest. The nest was not checked again until 6 June, at which time a single female *Polistes metricus* was present on the top of the nest. On 7 June it was determined that only three fifth-instar larvae and two eggs were present; the female *P. metricus* was still on top of the nest. On 8 June the female *P. metricus* had moved to the face of the nest (Fig. 1), where she was seen during eight of eighteen nest inspections until she was last seen on 28 June. Two of the larvae pupated on 12 June, and the third did so on 14 June. The adult wasp apparently cannibalized one of the eggs on 10 June, and she laid an egg (in a different nest cell) on 10 June and another on 17 June. One of the pupae was destroyed by a parasitoid on 29 June. Another pupa apparently yielded an adult on 30 June, but that adult was not seen. The third pupal cocoon remained intact, and the cell was subsequently found to contain evi-

dence of parasitoids. The eggs laid by the *P. metricus* eclosed into small larvae, but they failed to develop. The adult wasp was not seen to forage or to feed the larvae.

DISCUSSION

Much has been learned about *Polistes* subsequent to Snelling's (1952) observations. Of relevance to the observations reported here, it has been learned that pre-emergence nests may be usurped (forcefully taken over) by conspecific wasps that then become the colony queen. Perhaps the earliest report of aggressive intraspecific nest takeover was the graphic description by Yoshikawa (1955). Later it was learned that intraspecific usurpation can occur commonly in some populations (Klahn 1988; Makino and Sayama 1991), and still later it was suggested that conspecific nest usurpation may, in fact, reflect "sit and wait" behavior as a primary reproductive tactic (Starks 1998). (It can be noted that intraspecific usurpation is commonplace in yellowjackets [Greene 1991]). A similar behavior that is less well known but that may also be common in at least some *Polistes* populations is the takeover by a conspecific of an "orphan" nest. Death of a haplometrotic foundress due to predation or calamity seems the most likely cause of orphan nests. Perhaps the earliest report of such adoptions was by Kasuya (1982). Nonacs and Reeve (1993) present a thorough analysis of adoption of naturally-orphaned and transplanted (*i.e.*, artificially orphaned) nests in a population of *Polistes dominulus* (Christ), and they suggest that adoption could be a primary reproductive strategy. In all these cases, workers would provide care for unrelated brood being reared from eggs laid by the dominant co-nester or by the usurping/adopting queen.

Southern Europe is home to three species of socially parasitic (inquilinous) *Polistes* that forcefully evict or behaviorally dominate a foundress of another species (Weyrauch 1937; Cervo and Dani 1996). Intraspecific usurpation or adoption, as described above, seems a likely scenario for the evolution of such social parasitism, which would result in social parasite and host species being closely related (so-called "Emery's rule"). However, it has been demonstrated that the three species of obligate social parasite *Polistes* are monophyletic, and they are not more closely related to their hosts than they are to one another (Choudhary et al. 1994). Thus, social parasitism in *Polistes* has not evolved via speciation of social parasites from their hosts. What, then, might be a likely scenario for the origin of social parasitism in *Polistes*? The interspecific usurpations and adoptions reviewed and reported here suggest a possible framework. Elements of a plausible scenario include co-nesting of two species via any of the modes described above, commingling of chemical recognition profiles, further such commingling of recognition odors in mixed species overwintering groups as described by Snelling (1952), and delayed nesting as a primary reproductive tactic by one of the co-nesting species. A few successive successful generations could conceivably establish a trajectory.

In an amusing yet thought-provoking short note, Tordoff (1967) reports an unusual death of a caged bird. While scratching its head, the bird inadvertently caught a claw in the nictitating membrane of an eye, fell in its water dish, and drowned. Tordoff noted that the conditions could have been replicated in nature, and he further noted that the bird was scratching its head in a manner atypical for the species. He then queried whether this was an insignificant observation, or was it the very stuff of evolution? The same question can be asked about the observations reported here.

ACKNOWLEDGEMENTS

In the summer of 1971, after several increasingly assertive invitations, I went to the Los Angeles County Museum to meet Roy Snelling. "I hear you're going to work on ants," he said. "Yes," I replied. "Sit down," he said. I did. Whatever he was doing was set aside,

and for the next day and a half I was taken through a fast-paced, intensive short course in myrmecology. We discussed collecting and preservation. He taught me to point ants and kept me at it until my specimens at least came close to his high standards. He taught me to identify the common ants of California chaparral, with unknowns being put before me until I was batting over 500. At last satisfied (or seemingly satisfied) that I was started in the right direction, Roy wished me well in my research and said that he would help. One product that benefited from that collaboration was my dissertation. The most lasting outcome was "The ants of Chile" (Snelling and Hunt 1975). That work is 95% Roy's, of course, yet I am as proud of it as of anything I have done. Roy Snelling was a deeply respected mentor and colleague without whom my early successes would have been fewer and lesser. I have always been grateful.

Observations at Washington University's Tyson Research Center benefited from assistance with wasp observations by Bart Kensinger and Jessie Kossuth and nest box logistics by Jesse A. J. Hunt. In Raleigh, I was assisted in observations by Matthew K. Howe and Ellen E. Lentz and in nest box logistics by Yongliang Fan and, especially, Joe Flowers. I am particularly grateful to Freddie-Jeanne Richard, Université de Poitiers, for the photo that is Fig. 1. The observations reported here occurred during research supported by the U.S. National Science foundation.

LITERATURE CITED

Cervo, R. and F. R. Dani. 1996. Social parasitism and its evolution in *Polistes*. Pp. 98–112 *in* Turillazzi, S., and M. J. West-Eberhard eds. *Natural history and evolution of paper-wasps*. Oxford: Oxford University Press.

Choudhary, M., J. E. Strassmann, D. C. Queller, S. Turillazzi, and R. Cervo. 1994. Social parasites in polistine wasps are monophyletic - implications for sympatric speciation. *Proceedings of the Royal Society of London B* 257: 31–35.

Greene, A. 1991. *Dolichovespula* and *Vespula*. Pp. 263–304 *in* Ross, K. G., and R. W. Matthews eds. *The social biology of wasps*. Ithaca: Comstock Publishing Associates, Cornell University Press.

Hunt, J. H. and G. J. Gamboa. 1978. Joint nest use by two paper wasp species. *Insectes Sociaux* 25: 373–374.

———, B. A. Kensinger, J. Kossuth, M. T. Henshaw, K. Norberg, F. Wolschin, and G. V. Amdam. 2007. From casteless to castes – a diapause pathway underlies the gyne phenotype in *Polistes* paper wasps. *Proceedings of the National Academy of Sciences USA* 104: 14020–14025.

Kasuya, E. 1982. Take-over of nests in a Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). *Applied Entomology and Zoology* 17: 427–431.

Klahn, J. 1988. Intraspecific comb usurpation in the social wasp *Polistes fuscatus*. *Behavioral Ecology and Sociobiology* 23: 1–8.

Makino, S. and K. Sayama. 1991. Comparison of intraspecific nest usurpation between two haplometrotic paper wasp species (Hymenoptera: Vespidae: *Polistes*). *Journal of Ethology* 9: 121–128.

Nonacs, P. and H. K. Reeve. 1993. Opportunistic adoption of orphaned nests in paper wasps as an alternative reproductive strategy. *Behavioural Processes* 30: 47–59.

O'Donnell, S. and R. L. Jeanne. 1991. Interspecific occupation of a tropical social wasp colony (Hymenoptera: Vespidae: *Polistes*). *Journal of Insect Behavior* 4: 397–400.

Rau, P. and N. Rau. 1918. *Wasp studies afield*. Princeton: Princeton University Press.

Snelling, R. 1952. Notes on nesting and hibernation of *Polistes*. *Pan-Pacific Entomologist* 29: 177.

Snelling, R. R. and J. H. Hunt. 1975. The ants of Chile. *Revista Chilena de Entomologia* 9: 63–129.

Starks, P. T. 1998. A novel 'sit and wait' reproductive strategy in social wasps. *Proceedings of the Royal Society of London B* 265: 1407–1410.

Tordoff, H. B. 1967. An interesting case of mortality in the Gouldian Finch. *The Auk* 84: 604–605.

Weyrauch, W. K. 1937. Zur systematik und Biologie der Kuckuckswespen *Pseudovespa*, *Pseudovespula*, und *Pseudopolistes*. *Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere* 70: 243–290.

Yoshikawa, K. 1955. A polistine colony usurped by a foreign queen. Ecological studies of *Polistes* wasps II. *Insectes Sociaux* 2: 255–260.

J. HYM. RES.
Vol. 18(2), 2009, pp. 140–144

Mandibular Gland Chemistry of Two Nearctic Species of *Camponotus* (*Colobopsis*) (Hymenoptera: Formicidae)

RICHARD M. DUFFIELD, ROY R. SNELLING†, HENRY M. FALES AND MURRAY S. BLUM

(RMD) Department of Biology, Howard University, Washington, DC 20059, USA; email: rduffield@howard.edu
(RRS) Entomology Section, Emeritus, Natural History Museum of Los Angeles County, 900 Exposition Blvd, Los Angeles, CA 90007, USA
(HMF) Laboratory of Biophysical Chemistry, National Heart, Lung and Blood Institute, National Institutes of Health, Bethesda, Maryland, 20892, USA
(MSB) Department of Entomology, University of Georgia, Athens, GA 30602, USA

Abstract.—The chemistry of the mandibular gland secretions of three Nearctic species of carpenter ants of the subgenus *Colobopsis* was studied. No volatile compound was detected in worker mandibular secretions of *C. impressus* and *C. etiolates*. Worker secretions of *C. mississippiensis* were dominated by 2,6-dimethyl-5-heptene-1-ol and citronellol. Male head extracts of *C. impressus* and *C. mississippiensis* exhibited these two compounds and an additional volatile which was identified as mellein. Citronellol constituted 50% of the volatile components in each of these species.

Camponotus is a cosmopolitan genus of formicine ants. It is reported to have more than 1000 species worldwide split among several dozen subgenera (Bolton 1995a, 1995b). *Camponotus* species have diverse morphological adaptations as well as many unusual behavioral patterns. In North America north of Mexico there are approximately 50 species of *Camponotus* representing seven subgenera (Creighton 1950). Unique among the North American *Camponotus* are those that belong to the subgenus, *Colobopsis*. Major workers exhibit phragmosis: *i.e.* they insert their cylindrical heads into the opening of the nest entrance and act as living plugs. These diminutive species are arboreal, living in hollow stems and twigs.

Colobopsis was originally described as a genus separate from *Camponotus* (Mayr 1861). It was reclassified as a subgenus under *Camponotus* by Emery (1889) and has been more or less consistently so treated since then (Bolton 1995b). Subgenus *Colobopsis* is primarily Holarctic and mostly associated with northern hardwood forests. While numerous Southeast Asian and Melanesian species are currently placed in *Colobopsis*, they are improperly placed (R.Snelling, personal communication)

Camponotus mandibular gland secretions have been the focus of a number of chemical investigations. They exhibit a great diversity of chemical components. These investigations include those of Brand *et al.* (1973a, 1973b), Duffield and Blum (1975b), Lloyd et al. (1975), Duffield (1976), Jones and Fales (1983), Blum et al. (1987), Blum et al. (1988), Duffield et al. (1988), and Torres et al. (2001).

The isocoumarin, mellein, is a fungal metabolite found in *Aspergillus* species. Brand et al. (1973a, 1973b) were the first to identify mellein in ants. Since its initial identification in male mandibular gland secretions of *Camponotus*, mellein has been shown to be widely distributed in *Camponotus* (Duffield 1976). It has also been identified in the mandibular glands of *Polyrhachis doddi* Donisthorpe (Bellas and

† deceased.

Holldobler 1985) (Formicinae) and in *Rhytidoponera metallica* (Smith) (Ectatomminae) (Brophy et al. 1981). Mellein is a component of the trail pheromone of *Lasius fuliginosus* (Latreille) (Formicinae) (Kern et al. 1997) and in the rectal gland secretions of several species of *Camponotus* (Ubler et al. 1995). In contrast, mellein has also been identified in the anal secretions of a thrips (Blum et al., 1992); termites (Blum et al. 1982) as well as the hair pencil secretions of the danaine butterfly, *Idea leuconoe* (Erichson) (Nishida et al. 1996). Male bumblebee and wax moth secretions are also fortified with mellein (Kunesch et al. 1987). This abbreviated summary documents the rather widespread occurrence of mellein among different orders of insects.

The three terpenoids, citronellol, citronellic acid and 2,6-dimethyl-5-heptene-1-ol are also common ant mandibular gland secretions (Wheeler and Duffield 1988). 2,6-Dimethyl-5-heptene-1-ol has been previously identified in made mandibular gland secretions of *C. clarithorax* along with citronellic acid (Lloyd et al. 1975). 2,6-Dimethyl-5-heptene-1-ol has also been identified as the major constituent in the male mandibular gland secretions of *Lasius* (as *Acanthomyops*) *clavigerus* (Roger) (Regnier and Wilson 1968) and *L. umbratus* (Nylander) (Regnier and Wilson 1969).

We report the mandibular secretions of three species of *Colobopsis*.

MATERIALS AND METHODS

Collections of colonies of three species of *Colobopsis* were made for chemical analysis. Workers of *Camponotus etiolatus* Wheeler were collected from Live Oak and Uvalde Counties, Texas, by the senior author and the late myrmecologist, Dr. William Steel Creighton in January, 1973. *Camponotus impressus* (Roger) workers were collected from the vicinity of Paurotis Pond, Everglades National Park, Dade County, Florida (March, 1974). *Camponotus mississippiensis* Smith was collected along Whitehall Road, Clark County, Georgia and from the Oconee National Forest, Georgia during November–December, 1973. Voucher specimens were deposited in the entomology collections at the Georgia Natural History Museum, University of Georgia, Athens, Georgia, USA.

Before excising the ant heads, each colony was cooled at 4°C for several hours. Ant heads were removed with forceps and placed in spectral grade methylene chloride for 24 hours. Separate extracts were made of minor workers, major workers and male heads for *C. impressus* and *C. mississippiensis*. Only minor worker head extracts were obtained for *C. etiolatus*. Male head extracts consisted of 20–30 heads. Minor worker extracts consisted of several hundred heads and major worker head extracts consisted of approximately 200 heads, depending upon the numbers available. The solvent for each extract was drawn off and dried with sodium sulfate. Each sample was concentrated by room evaporation and analyzed by gas chromatography-mass spectroscopy.

Worker mandibular glands of *C. mississippiensis* were excised using a dissecting microscope and extracted with methylene chloride. Extracts were analyzed on a gas chromatography.

The concentrated samples were analyzed on a LKB 9000 combined gas chromatograph-mass spectrometer (GC-MS) using10% SP-1000 as the stationary phase. The column was temperature programmed at 10°C/min. to 200°C. Mass spectra and retention times of mellein, citronellol and 2,6-dimethy-5-hepten-1-ol were consistent with those of authentic standards.

RESULTS

Compound number 1 (Table 1) showed a molecular ion at m/e 142, and ions at m/e 124, 109, 95, 82, 69, 67, 55 and 41 suggesting it was an unsaturated, terpenoid alcohol. An authentic sample of 2,6-dimethyl-5-heptene-1-ol had a retention time and mass spectrum identical to those of the unknown. The second compound

Table 1. Volatile components in the mandibular gland secretions of three species of *Camponotus* subgenus *Colobopsis*.

Species/Volatile compounds	1	2	3	4	5
C. etiolates (minor workers)	–	–	–	–	–
C. impressus (minor workers)	–	–	–	–	–
C. impressus (males)	+	+[a]	+	–	+
C. mississippiensis (minor workers)	+	+[a]	–	+	–
C. mississippiensis (males)	+	+	+	–	–

Compound 1. 2,6-dimethyl-5-heptene-1-ol; Compound 2. citronellol; Compound 3. mellein; Compound 4. citronellic acid; Compound 5 Unknown M.W. 154.
a = 50% of the volatile components.

gave a molecular ion at m/e 156 and strong ions at 41 and 69 suggesting an acyclic terpene. Ions were observed at 138, 123, 109, 95, 82, 81, 69, 67, 56, 55, and 41. An authentic sample of citronellol gave identical retention times and mass spectra as the unknown.

The third compound exhibited a molecular ion at 178 and ions at m/e 160, 149, 134, 132, 111, 106, 105, 104, 79, 77, 53, 52, 51, 43 and 41. The compound was identified as mellein. Compound 4 had a molecular ion at m/e 170 and fragment ions at m/e 41 and 69 indicating an acylic terpene. An authentic sample of citronellic acid had a retention time and mass spectrum identical to those of the unknown.

The results of the chemical analyses of the three species of *Colobopsis* are presented in Table 1. No detectable volatiles were found in the head extracts of *C. etiolatus*. This may have been due to the limited number of heads extracted. While no volatile compounds were detected in the minor worker head extracts of *C. impressus*, male head extracts contained mellein, citronellol and 2,5-dimethy-5-hepten-1-ol. It is surprising that no volatiles were detected in the worker extracts. The worker head extracts contained many more heads compared to the male head extracts.

Chemical analyses of *C. mississippiensis* minor workers and males exhibited two volatiles in common, citronellol and 2,6-dimethy-5-hepten-1-ol. Each extract also contained an additional volatile. Workers contained citronellic acid and males contained mellein.

The gas chromatogram of the excised mandibular gland extracts of *C. mississippiensis* workers exhibited two volatile compounds whose retention times matched those of authentic citronellol and 2,5-dimethy-5-hepten-1-ol. We concluded that the volatile compounds in the head extracts were mandibular gland products.

DISCUSSION

Formicine genera of ants are unlike many other genera of ants where worker males and females exhibit the same volatile mandibular gland compounds, and in which species in the same genus often exhibit the same mandibular gland components. Several formicine genera have been shown to exhibit male-specific mandibular gland components. These include *Lasius* (Law et al. 1965) *Camponotus* (Brand et al. 1973a, b) and *Oecophylla* (Bradshaw et al. 1979), all in the subfamily Formicinae.

Camponotus is an ideal genus to study from a chemo-systematic standpoint. In some species males have multi-component mandibular gland secretions absent in workers and female reproductives. Other species exhibit the same components in males, female reproductives and workers (Duffield 1976). In this investigation, *C. mississippiensis* males and workers both have mandibular gland secretions that contain volatile compounds. While they

share two compounds, each has one distinctive compound.

Based on the volatile mandibular gland secretions of the two *Colobopsis* species, they form a group separate from other North American *Camponotus*. They are similar to other *Camponotus* in that they have a male mandibular gland secretion that contains mellein. The *Colobopsis* species in one sense are similar to the male mandibular gland extracts of *C. clarithorax* Creighton which are also fortified with citronellol, and 2,6-dimethyl-5-heptene-1-ol. *Camponotus clarithorax* is contrastingly different in that it exhibits a number of additional compounds and no mellein.

ACKNOWLEDGMENTS

We would like to acknowledge the assistance of the late Dr. William Steel Creighton for his help in collecting *C. etiolatus*. The authors acknowledge and appreciate the use of the gas chromatograph-mass spectrometry equipment at the National Institutes of Health, Heart, Blood and Lung Institute.

LITERATURE CITED

Bellas, T. and B. Hölldobler. 1985. Constituents of mandibular and Dufour's glands of an Australian *Polyrhachis* weaver ant. *Journal of Chemical Ecology* 11: 525–538.

Blum, M. S., R. Foottit, and H. M. Fales. 1992. Defensive chemistry and function of the anal exudate of the thrips *Haplothrips leucanthemi*. *Comparative Biochemistry and Physiology* 102C: 209–211.

———, T. H. Jones, D. F. Howard, and W. L. Overal. 1982. Biochemistry of termite defenses: *Coptotermes, Rhinotermes* and *Cornitermes*. *Comparative Biochemistry and Physiology* 71B: 731–733.

———, L. Morel, and H. M. Fales. 1987. Chemistry of the mandibular gland secretion of the ant *Camponotus vagus*. *Comparative Biochemistry and Physiology* 86B: 251–252.

———, R. R. Snelling, R. M. Duffield, H. Hermann Jr, and H. A. Lloyd. 1988. Mandibular gland chemistry of *Camponotus* (*Myrmothrix*) *abdominalis*: Chemistry and chemosystematic implications (Hymenoptera: Formicidae). Pp. 481–490 *in* Trager, J. C. ed. *Advances in Myrmecology*. E. Brill Pub., New York.

Bolton, B. 1995a. A taxonomic and a zoogeographical census of extant ant taxa (Hymenoptera: Formicidae). *Journal of Natural History* 29: 1039–1056.

———. 1995b. *A New General Catalogue of the Ants of the World*. Cambridge, MA: Harvard University Press.

Bradshaw, J. W. S., R. Baker, and P. E. Howse. 1979. Multicomponent alarm pheromones in the mandibular glands of major workers of the African weaver ant, *Oecophylla longinoda*. *Physiological Entomology* 4: 15–25.

Brand, J. M., R. M. Duffield, J. G. MacConnell, M. S. Blum, and H. M. Fales. 1973a. Caste-specific compounds in male carpenter ants. *Science* 179: 388–389.

———, H. M. Fales, E. A. Sokoloski, J. G. MacConnell, M. S. Blum, and R. M. Duffield. 1973b. Identification of mellein in the mandibular gland secretions of carpenter ants. *Life Sciences* 13: 201–211.

Brophy, J. J., G. W. Cavill, and W. D. Plant. 1981. Volatile constituents of an Australian ponerine ant *Rhytidoponera metallica*. *Insect Biochemistry* 11: 307–310.

Brown, W. V. and B. P. Moore. 1979. Volatile secretory products of an Australian formicine ant of the genus *Calomyrmex* (Hymenoptera: Formicidae). *Insect Biochemistry* 9: 451–460.

Creighton, W. S. 1950. The ants of North America. *Bulletin of the Museum of Comparative Zoology, Harvard* 104: 1–585.

Duffield, R. M. and M. S. Blum. 1975. Identification, role and systematic significance of 3-octanone in the carpenter ant, *Camponotus schaefferi* Whr. *Comparative Biochemistry and Physiology* 51B: 281–282.

———. 1976. *A comparative study of the mandibular gland chemistry of formicine and ponerine ant species*. Ph.D. Dissertation, University of Georgia, Athens, Ga.

———, J. W. Wheeler, and R. R. Snelling. 1988. Mellein in the mandibular glands of worker *Camponotus ferrugineus* (Fabr.): An anomoly in the subgenus *Camponotus*. Pp. 475–480 *in* Trager, J. C., ed. *Advances in Myrmecology*. E. Brill Pub., New York.

Emery, C. 1889. Viaggio di Leonardo Fea in Birmania e regioni vicine. 20. Formiche di Birmania e del tenasserim raccolte da Leonardo Fea (1885–87). *Annali del Museo Civico di Storia Naturale di Genova* 7 [27]: 485–520.

Haak, U., B. Hölldobler, H. J. Bestmann, and F. Kern. 1996. Species-specificity in trail pheromones and Dufour's gland contents of *Camponotus atriceps* and *C. floridanus* (Hymenoptera: Formicidae). *Chemoecology* 7: 85–93.

Jones, T. H. and H. M. Fales. 1983. E-6-(1-pentenyl)-2H-pyran-2-one from carpenter ants (*Camponotus* spp). *Tetrahedron Letters* 24: 5439–5440.

Kern, F., R. W. Klein, E. Janssen, H. J. Bestmann, A. B. Attygalle, D. Schafer, and U. Maschwitz. 1997. Mellein, a trail pheromone component of the ant *Lasius fuliginosus*. *Journal of Chemical Ecology* 23: 779–792.

Kunesch, G., P. Zagatti, A. Pouvreau, and R. Cassini. 1987. A fungal metabolite as the male wing gland pheromone of the bumblebee wax moth, *Aphomia sociella* L. *Zeitschrift für Naturforschung* 42: 657–659.

Law, J. H., E. O. Wilson, and J. A. McCloskey. 1965. Biochemical polymorphism in ants. *Science* 149: 544–545.

Lloyd, H. A., M. S. Blum, and R. M. Duffield. 1975. Chemistry of the male mandibular gland secretion of the ant, *Camponotus clarithorax*. *Insect Biochemistry* 5: 489–494.

Mayr, G. 1861. *Die Europäischen Formiciden (Amerisen) Wien*. 80 pp. [(31,xii).1861.]

Nishida, R., S. Schulz, C. S. Kim, H. Fukami, Y. Kuwahara, K. Honda, and N. Hayashi. 1996. Male sex pheromone of a giant danaine butterfly, *Idea leuconoe*. *Journal of Chemical Ecology* 22: 949–972.

Regnier, F. E. and E. O. Wilson. 1968. The alarm-defence system of the ant *Acanthamyops claviger*. *Journal of Insect Physiology* 14: 955–970.

——— and ———, 1969. The alarm defense system of the ant *Lasius alienus*. *Journal of Insect Physiology* 15: 893–898.

Torres, J. A., R. R. Snelling, M. S. Blum, R. C. Flournoy, T. H. Jones, and R. M. Duffield. 2001. Mandibular gland chemistry of four Caribbean species of *Camponotus* (Hymenoptera: Formicidae). *Biochemical Systematics & Ecology* 29: 673–680.

Ubler, E., F. Kern, H. J. Bestmann, B. Hölldobler, and A. B. Attygalle. 1995. Trail pheromone of two formicine ants, *Camponotus silvicola* and *C. rufipes* (Hymenoptera: Formicidae). *Naturwissenschaften* 82: 523–525.

Wheeler, J. W. and M. S. Blum. 1973. Alkylpyrazine alarm pheromones in ponerine ants. *Science* 182: 501–503.

——— and R. M. Duffield. 1988. Pheromones of Hymenoptera and Isoptera. Pp. 59–206 *in* Morgan, E. D. and N. B. Mandava, eds. *Handbook of Natural Pesticides, Part B. Pheromones*. Vol IV. CRC Press.

J. HYM. RES.
Vol. 18(2), 2009, pp. 145–150

Venom Alkaloids from Some *Monomorium* Species

ALEXANDER J. SNYDER, TAPPEY H. JONES*, GORDON C. SNELLING AND ROY R. SNELLING

(AJS, THJ) Department of Chemistry, Virginia Military Institute, Lexington, Virginia 24450-0304, USA; email: jonesth@vmi.edu
(GCS) 13161 Rancherias Rd. Apple Valley, California 92308, USA
(RRS) Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, USA, deceased May 12, 2008

Abstract.—The extracts of eight species of *Monomorium* collected from 1996 to 2003 were analyzed and their characteristic venom alkaloids were identified. In each case, the peculiarity of the compounds in each species is related to previously described Myrmicine ant venoms. The taxonomic utility of these analyses is discussed.

Saturated nitrogen heterocycles have been known for over thirty years as components of the venoms of ants in the genera *Monomorium* and *Solenopsis* (Jones et al. 1982b), and these alkaloids play a well-documented defensive role in *Monomorium* species (Andersen et al. 1991). While different species of ants may have the same alkaloids, the alkaloid composition of a particular species seems to be characteristic, varying only with the age of the ants (Deslippe and Guo 2000). Comparisons of the alkaloid composition in *Solenopsis* species have been made a number of times (Brand et al. 1972; MacConnell et al. 1976; Vander Meer and Lofgren 1988). Conservatively, there are ca. 300 species of *Monomorium* worldwide (Heterick 2001), and the chemistry of a number of individual species has been reported (Jones et al. 1982b, 1989, 1990a,b, 2003; Andersen et al. 1991; Don et al. 2001). Although indolizidines, piperidines, and pyrrolizidines have been found in *Monomorium* species, 2,5-dialkylpyrrolidines are the most commonly detected alkaloids in this genus. There have been comparative studies of the alkaloids of some groups of *Monomorium* species in the United States, New Zealand and Africa (Jones et al. 1982a, 1988b, 2003), with some interest in the biological roles of these compounds; *i.e.* taxonomic value and investigation of their means to serve as defense and in predation.

There are several common structural features of the natural 2,5-disubstituted pyrrolidines found in *Monomorium* species. Most notably, the natural pyrrolidines have odd-numbered carbon skeletons and the predominance of the *trans* configuration of the ring substituents. These characteristics are easily elucidated by mass spectra in the first case and by gas chromatographic comparison with synthetic *cis/trans* mixtures in the second (Pedder et al. 1976; Jones et. al. 1979). Another important characteristic of natural pyrrolidines found in *Monomorium* species is the double bond position in the unsaturated alkyl substituents. When present, the alkyl double bonds are always terminal. Traditionally, the positions of these olefins have been verified by derivization and gas chromatography comparison with synthetic material (Jones et al. 1982b, 1988a).

In this paper, we report various alkaloids found in eight different *Monomorium* species collected in Australia, Indonesia, and Kenya from 1996 to 2003. The *Monomorium* species collected in Indonesia have yet to

* To whom correspondence should be addressed.

Table 1. Alkaloids identified from *Monomorium* species.

Species	RRS #	1	2	3	4	5	6	7	8	9	10	11
M. leae	96-449			+								
M. emersoni	01-480	4	78	17								
M. sydneyense	01-032					+						
M. rosae	01-115				+							
M. leopoldinum	03-128							1	2			
M. bifidum	03-141						2*			1	3	94*
M. species 1	98-013		1	2								
M. species 4	98-151				+							

+ = Only alkaloid detected.
* = Multiple stereoisomers detected.

be completely described, and are referred to as *M.* species 1 and *M.* species 4. In all cases except for two described species, the alkaloids are mixtures of previously reported 2,5-dialklypyrrolidines, whose structures were established by a direct comparison with synthetic samples available from previous work.

METHODS AND MATERIALS

Ants.—Collections of 10–50 workers of each species listed below were placed in a vial containing a small amount of methanol for subsequent chemical analysis. Voucher specimens of all samples are deposited in the collection of the Los Angeles County Museum of Natural History, Los Angeles, CA. RRS's collection numbers for each sample are listed in Table 1.

Monomorium leae Forel, Picadilly Circus, Brindabella Range, A.C.T., Australia;

M. emersoni Gregg, CSIRO-TERC, Berrimah, Northern Territory, Australia, 12.411°S 130.92°E, ca. 80 ft. Secondary subtropical savannah;

M. sydneyense Forel, Reef Point, Murramarang National Park; N.S.W., Australia 35.72°S 150.25°E. 0–50 m. Dry sclerophyll;

M. rosae Santschi, Laikipia Distr. Mpala Ranch, confluence of Ewaso Ng'iro and Ewaso Narok, Kenya 0.53°N 38.86°E, *Acacia* xanthophloem and *Ficus*;

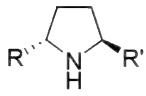
M. leopoldinum Forel, Kakamega Distr. S edge, Kalunya Glade, Kenya 0.245°N 34.870°E;

M. bifidum Heterick, CSIRO-TERC, Berrimah, Northern Territory, Australia, 12.411°S 130.92°E, ca. 25 m. Secondary subtropical savannah;

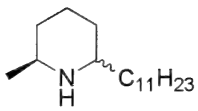
M. sp 1 and *M.* sp 4; PT. Freeport Concession, Siewa camp, Irian Jaya, Indonesia 03.04°S 136.38°E, 65 m; lowland secondary rainforest, along Wapoga River.

Chemical analysis.—Gas chromatography-mass spectrometry was carried out in the EI mode using a Shimadzu QP-5000 GC/MS equipped with a RTX-5, 30 m × .032-mm i.d. column. The instrument was programmed from 60°C to 250°C at 10°/min. Identification of the alkaloids was confirmed by direct comparison of their mass spectra and retention times with those of synthetic samples available from previous work (Fig. 1; Table 1)

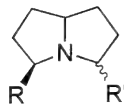
2-Butyl-5-tridecylpyrrolidine (**5**). A Stetter condensation of tetradecanal and 1-hepten-3-one (Jones et al. 1988a) provided 5,8-henecosadione in the usual manner: HRMS: Calculated for $C_{21}H_{41}O_2$ (M+1), 325.3107; observed 325.3113. Subsequent reductive amination (Jones et al 1988a) in the usual manner provided a 1:1 mixture of *cis* and *trans* 2-Butyl-5-tridecylpyrrolidine (**5**). MS *m/z* (rel%): 309(1, M^+), 308(2), 252(75), 152(3), 127(3), 126(100), 82(10, 55(12); HRMS: Calculated for $C_{21}H_{44}N$ (M+1), 310.3474; observed 310.3481. The single alkaloid detected in *M. sydneyense* had a mass spectrum and retention time identical with those of the second eluting, *trans* isomer of the synthetic mixture of **5**.



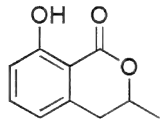
1: R = C_6H_{13}, R' = C_9H_{19}
2: R = $C_4H_8CH{=}CH_2$, R' = C_9H_{19}
3: R = $C_4H_8CH{=}CH_2$, R' = $C_7H_{14}CH{=}CH_2$
4: R = C_4H_9, R' = C_7H_{15}
5: R = C_4H_9, R' = $C_{13}H_{27}$
6: R = $C_4H_8CH{=}CH_2$, R = $C_5H_{10}CH{=}CH_2$



7: *cis*
8: *trans*



9: R = $C_2H_4CH{=}CH_2$, R' = $C_2H_4CH{=}CH_2$
10: R = C_3H_7, R' = C_5H_{11}
11: R = $C_2H_4CH{=}CH_2$, R' = $C_4H_8CH{=}CH_2$



Mellien

Fig. 1. Compounds detected in the extracts of some *Monomorium* species Australia, Indonesia, and Kenya.

M. bifidum. GC/MS analysis of the extracts of *M. bifidum* showed five nitrogen containing components in the ratios shown in Table 1. Both isomers of **6** were identified from comparison to previously published spectra (Jones et al. 1989). **9:** MS *m/z* (rel%): 219 (1,M+), 166(10), 70(9), 68(22), 67(25), 164(100), 124(10), 122(5), 41(70); **10:** MS *m/z* (rel%): 247(1,M+), 206(3), 192(80), 164(100), 124(20), 122(8), 70(10), 68(17), 67(25), 41(90); **11:** MS *m/z* (rel%): 247(1,M+), 206(1), 192(60), 164(100), 110(15), 108(4), 70(14), 68(20), 67(31), 41(92). Additionally approximately 1% of mellein was detected. Hydrogenation of a small sample of the extract over PtO_2 converted **9** to 3,5-dibutylpyrrolizidine (Garraffo et al. 1993), and **11** to the isomers of 3-butyl-5-hexylpyrrolizidine (Don and Jones 1993) which were available from previous studies.

RESULTS AND DISCUSSION

Since at least 1982, one of us (THJ) has conducted chemical analyses of ants RRS had collected. After the original chemical studies of fire ants (*Solenopsis*, subgenus *Solenopsis* spp) demonstrated differences in venom alkaloids between different species (MacConnell et al. 1976), the exocrine

chemistry of ants has been recognized as a valid taxonomic character in a number of differing groups of ants, barring some mitigating factor such as dependence on dietary sources. Often, a particular species would have some unique chemistry and RRS would then know of other related species and plan to get those on future collecting trips. In those cases we would simply wait until he had done so. The comparative study of a number of African *Monomorium* species (Jones et al. 2003) is a good example of this *modus operandi* where the collections were made over several trips. In this report we present the chemistry of the venom alkaloids of eight species of *Monomorium* from Australia, Indonesia and Kenya that were to have been markers or starting points for future sets of collections of related species, and the subsequent investigations would have most likely resulted in three separate manuscripts. The results described in this report are presented according to the structures of the venom alkaloids in the species that were examined.

The extracts of *M. leae*, *M. emersoni*,and *M.* species 1 all contained the well-known nineteen carbon 2,5-dialkyl C_6, C_9 pyrrolidines, **1**, **2**, and **3**. These compounds all have the *trans* stereochemistry regarding the attachment of the alkyl groups to the central ring, and vary only in the number of terminal carbon-carbon double bonds on their side chains. Compounds **1**, **2**, and **3** are exclusive components in the venoms of North American *Monomorium* species, in contrast with the more complex mixtures found in *Monomorium* species from New Zealand, for example. Although **1**, **2**, and **3** have also been found as concomitants with homologous bicyclic alkaloids and with alkaloids of varied carbon chain lengths in African, Australian, and New Zealand *Monomorium* species. In Australian and North American species, these compounds repel larger ants (Jones et al. 1982b; Jones et al. 1988b; Jones et al. 2003).

The extracts of *M. rosae* and *M.* species 4 contains only *trans*- 2-butyl-5-heptylpyrrolidine **4**, a previously described compound typically found in various *Solenopsis* and *Monomorium* species. Interestingly, compound **4** was actually first detected in thief ants, *Solenopsis* (*Diplorhoptrum*), as a component of their poison glands (Blum et al. 1980; Jones et al. 1982a). Compound **4** was studied more extensively after its detection in the well-known *Solenopsis fugax*, where it was shown to be a repellant of several genera of much larger ants (Blum et al. 1980). Compound **4** has also been detected as a component of a complex mixture of pyrrolidines in various *Monomorium* species, most notably *M. latinode and M. indicum*. Compound **4** was shown to be a minor component of *M. latinode's* venom (Jones et al. 1982b) and *M. indicum*, which possesses the most complex mixture of dialkylpyrrolidines ever detected in a *Monomorium* species (Jones et al. 1989). Uniquely, we were able to show that compound **4** was a single component venom alkaloid in *M. rosae* and *M.* species 4, contrasting with previously published studies involving *Monomorium* species containing compound **4**. Moreover, these *Monomorium* species were collected in disparate areas of the world (*M. rosae* – Kenya, *M.* species 4 – Indonesia), raising the question of why these two ants share the chemical similarity of having compound **4** as the sole alkaloid in their venom.

trans-2-Butyl-5-tridecylpyrrolidine **5** was detected in *Monomorium sydneyense*, a species native to the continent of Australia. This is the first report of compound **5**: a C_{21} pyrrolidine where direct comparison with synthetic material established its overall structure and *trans* stereochemistry. Although long carbon chains ($> C_{15}$) are rare in *Monomorium* species, it has been observed that other Australian *Monomorium* species contain the compound 2-ethyl-5-tridecylpyrrolodine (C_{19}) as a well-known component of their venom (Andersen et al. 1991). Interestingly, the venom alkaloids found in these Australian *Monomorium*

species resemble the 2-methylpiperidines commonly found in fire ants. A structural theme in fire ants is that the more potent venoms have longer side chains (Brand et al. 1972), which may be analogous with these Australian *Monomorium* species.

The extract of *M. leopoldinum* contained both the *cis* and *trans* isomer of 2-methyl-6-undecylpiperidine (compounds **7** and **8** respectively). Compounds **7** and **8** are 6 membered, nitrogen containing, di-substituted rings that are commonly found in thief ants, such as *S. carolinensis* (Jones et al. 1982a). Our particular findings with *M. leopoldinum* are unique because we found both the *cis* and *trans* isomers (compounds **7** and **8**) in equal amounts in a *Monomorium* species as opposed to a *Solenopsis* species. Initially, this finding led one of us (THJ) to suggest that *M. leopoldinum* was actually a *Solenopsis* species. However, RRS wittily responded in an email exchange to this attempted classification by a chemist with the following statement:

> "Well, I surely do hate to toss icy water on you all's pretty notions, but this critter is a genuine, honest to gosh *Monomorium*! In fact, nearly as I can figure, it is *M. leopoldinum* Forel. So, put that in your gas chromatograph and smoke it."

Although 2,6-dialkylpiperidines have previously been reported in the venom of *M. delagoense* (Jones et al. 1990b) this is the first report of a 2-methyl-6-alkylpiperidine, a structural type so typical of *Solenopsis* species, in a *Monomorium* species.

Of the venoms described in this paper, the venom of *M. bifidum* has proved to be the most complex. The major component (ca. 94%) of the venom of *M. bifidum* was a four to one mixture of the *exo*, *exo*-3-butenyl-5-hexenylpyrrolizidine and the *exo,endo*-3-butenyl-5-hexenylpyrrolizidine (**11**), along with ca. 5% exo,exo-3,5-dibutenylpyrrolizidine (**9**). Hydrogenation of a small sample of this extract converted **11** and **9** to the previously described 3-butyl-5-hexylpyrrolizidine (Jones et al. 1991; Don and Jones 1993) and 3,5-dibutylpyrrolizodine respectively (Garraffo et al. 1993), which were available from previous studies. In addition, trace amounts of 5-butyl-3-pentylpyrrolizidine (**10**) and 2-hexenyl-5-heptenylpyrrolidine (**6**), the monocyclic homologue of **11**, were also detected (Jones et al. 1989). The presence of **6** supports the terminal double bonds in **9** and **11**. This mono to bicyclic analogy is consistent with other *Monomorium* species, as it has been observed in *M. smithii* (Jones et al. 1990a). Additionally, small amounts of mellien were detected in the extract of *M. bifidum*. This compound is commonly found in numerous *Camponotus* species (Brand et al. 1973; Duffield et al. in Press). Mellien has never been reported from *Monomorium* or any other Myrmicine species, raising the possibility that it may be a dietary artifact in *M. bifidum*.

CONCLUSION

The genus *Monomorium* is distributed worldwide with approximately three hundred described species and a seemingly infinite number of undescribed ones. As one would expect from a genus of such taxonomic diversity, identification of the various species and forms can be extremely challenging. The results presented here and in previous papers demonstrate the potential taxonomic application of the use of venom alkaloids for identification purposes among the various *Monomorium* species. This initial chemical overview of work by RRS demonstrates the need for additional studies involving chemotaxonomic investigations of related species.

LITERATURE CITED

Andersen, A. N., M. S. Blum, and T. H. Jones. 1991. Venom alkaloids in *Monomorium "rothsteini"* Forel repel other ants: is this the secret to success by *Monomorium* in Australian ant communities? *Oecologia* 88: 157–160.

Blum, M. S., T. H. Jones, B. Hölldobler, H. M. Fales, and T. Jaouni. 1980. Alkaloidal venom mace:

offensive use by a thief ant. *Naturwissenschaften* 67: 144–145.

Brand, J. B., M. S. Blum, H. M. Fales, and J. G. MacConnell. 1972. Fire ant venoms: Comparative analysis of alkaloidal components. *Toxicon* 10: 259–271.

Brand, M. J., R. M. Duffield, J. G. MacConnell, M. S. Blum, and H. M. Fales. 1973. Caste-specific compounds in male carpenter ants. *Science* 179: 388–389.

Deslippe, R. J. and Y.-J. Guo. 2000. Venom alkaloids of fire ants in relation to worker size and age. *Toxicon* 38: 223–232.

Don, A. W. and T. H. Jones. 1993. The stereochemistry of 3-butyl-5-(5-hexenyl)-pyrrolizidine from populations of *Monomorium antarcticum* (Smith) (Hymenoptera: Formicidae) and its possible role as a unique taxonomic character. *New Zealand Entomologist* 16: 45–48.

Duffield, R. M., R. R. Snelling, H. M. Fales, and M. S. Blum. Mandibular Gland Chemistry of Two Nearctic Species of *Camponotus* (*Colobopsis*) (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* (in Press).

Garraffo, H. M., T. F. Spande, J. W. Daly, A. Baldessari, and E. G. Gros. 1993. Alkaloids from Bufonid toads (Melanophryniscus): Decahydroquinolines, Plumiliotoxins and Homopumiliotozins, Indolizidines, Pyrrolizidines, and Quinolizidines. *Journal of Natural Products* 56: 357–373.

Heterick, B. E. 2001. Revision of the Australian ants of the genus *Monomorium* (Hymentoptera: Formicidae). *Invertebrate Taxonomy* 15: 353–459.

Jones, T. H., M. S. Blum, and H. M. Fales. 1982a. Ant venom alkaloids from *Solenopsis* and *Monomorium* species. *Tetrahedron* 38: 1949–1958.

———, ———, R. W. Howard, C. A. McDaniel, H. M. Fales, and M. B. DuBois. 1982b. Venom chemistry of ants in the genus *Monomorium*. *Journal of Chemical Ecology* 8: 285–300.

———, ———, A. N. Andersen, and P. Escoubas. 1988a. Novel 2-Ethyl-5-alkylpyrrolidines in the venom of an Australian ant of the genus *Monomorium*. *Journal of Chemical Ecology* 14: 35.

———, S. M. Stahly, A. W. Don, and M. S. Blum. 1988b. Chemotaxonomic implications of the cenom chemistry of some *Monomorium "antarcticum"* populations. *Journal of Chemical Ecology* 14: 2197–2212.

———, M. S. Blum, P. Escoubas, and T. M. Musthak Ali. 1989. Novel pyrrolidines in the venom of the ant *Monomorium indicum*. *Journal of Natural Products* 52: 779–784.

———, A. Laddago, W. A. Don, and M. S. Blum. 1990a. A novel (5E,9Z)-dialkylindolizidine from the ant *Monomorium smithii*. *Journal of Natural Products* 53: 375–381.

———, M. S. Blum, and H. G. Roberston. 1990b. Novel dialkylpiperidines in the venom of the ant *Monomorium delagoense*. *Journal of Natural Products* 53: 429–435.

———, ———, H. M. Fales, C. R. Brandao, and J. Lattke. 1991. Chemistry of venom alkaloids in the ant genus *Megalomyrmex*. *Journal of Chemical Ecology* 17: 1897–1908.

———, V. E. Zottig, H. G. Robertson, and R. R. Snelling. 2003. The venom alkaloids from some african *Monomorium* species. *Journal of Chemical Ecology* 29: 2721–2727.

MacConnell, J. G., M. S. Blum, W. F. Buren, R. N. Williams, and H. M. Fales. 1976. Fire ant venoms: Chemotaxonomic correlations with alkaloidal compositions. *Toxicon* 14: 69–78.

Vander Meer, R. K. and C. S. Lofgren. 1988. Use of chemical characters in defining populations of fire ants, *Solenopsis saevissima* complex, (Hymenoptera: Formicidae). *Florida Entomologist* 71: 323–332.

J. HYM. RES.
Vol. 18(2), 2009, pp. 151–166

The Biology of *Hoplitis (Robertsonella) simplex* (Cresson), with a Synopsis of the Subgenus *Robertsonella* Titus

JOHN L. NEFF

Central Texas Melittological Institute, 7307 Running Rope, Austin, Texas 78731, USA;
email: jlnatctmi@yahoo.com

Abstract.—Three species are recognized in *Hoplitis (Robertsonella): H. micheneri* Mitchell, *H. nemophilae* Neff, and *H. simplex* Cresson. *Hoplitis nemophilae* is described and a key is provided for the subgenus. The nesting biology of *H. simplex* is described, along with notes on the biology of the other species. *Hoplitis simplex* is a vernal bee that gathers mud to construct nests in pre-existing cavities. It appears to be an oligolege of the Boraginaceae: Hydrophylloideae and constructs 1–3 cells per day. The last larval instar commences defecation the day after the last larval molt and initiates construction of the operimentum (a secreted lining on the anterior cell partition) well before the completion of feeding.

Robertsonella Titus is a small group of osmiine bees of eastern North America (Tamaulipas, Mexico to Connecticut, USA). Although originally given generic status, it currently is considered to be a subgenus of *Hoplitis* Klug (Hurd and Michener 1955; Michener 2007). While studying the pollination biology of *Nemophila phacelioides* Nutt. (Boraginaceae: Hydrophylloideae) in central Texas, I commonly encountered two *Robertsonella* species at *N. phacelioides* flowers. One species was particularly abundant at the Brackenridge Field Laboratory (BFL) of the University of Texas, in Austin, Texas and was found to regularly nest in small diameter trap nests. Since nothing had been reported on the nests of any *Robertsonella* species, a study was undertaken of its nest biology.

Problems arose when attempting to identify the two species. Mitchell (1962), recognized two species of *Robertsonella* from Texas: *Hoplitis simplex* (Cresson) and *Hoplitis gleasoni* (Titus). He noted that he might have errantly associated the sexes of *H. simplex* when he described what he believed to be the previously unknown male of that species. If true, this would require a new name for his new male. An analysis of the distribution of males of the species of *Robertsonella* was undertaken to resolve this problem. Here I report on the results of that analysis along with data on the biology of *H. simplex*.

MATERIALS AND METHODS

All timings of foraging and nest construction were performed at Brackenridge Field Laboratory (BFL) of the University of Texas at Austin (30.285° N 97.781° W) with either a handheld stopwatch or a digital watch. Activities were timed to the nearest second for nest provisioning and construction and to 0.1 sec for foraging behavior at flowers. Casual observations of *Hoplitis simplex* began in 1982 with timings of provisioning and nest construction occurring during the springs of 1986–1990 and 1994 and 1995. The possibility for observations of *H. simplex* at BFL were greatly curtailed after 1999 when a deer population explosion devastated the forbs at BFL, leading to a precipitous decline of the *H. simplex* population. Detailed observations of larval development and cocoon construction were made using split trap nests in 1987 and 1988. Morphological terminology follows Michener (2007). Distributions

are recorded at the county level. Abbreviations are as in Neff (2004). Statistics were calculated with JMP® and are presented as the mean ± 1 s. d.

Institutions or collections where paratypes are deposited, as well as the sites for other material examined, are as follows: American Museum of Natural History, New York, New York (AMNH); Snow Entomology Museum, University of Kansas, Lawrence, Kansas (KSEM); Museum of Entomology, Florida State University, Tallahassee, Florida (FSCA): Texas A & M University Insect Collection, College Station, Texas (TAMU); U. S. National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); Utah State University Bee Biology and Systematics Laboratory, Logan, Utah (BLCU); North Carolina State University Insect Collection, Raleigh, North Carolina (NCSU); Purdue University Insect Collection, West Lafayette, Indiana (PURC); M. S. Arduser Collection, St. Louis, Missouri (MSAC); Central Texas Melittological Institute, Austin, Texas (CTMI); Brackenridge Field Lab Collection, The University of Texas at Austin, Austin, Texas (BFLC).

TAXONOMIC HISTORY

Robertsonella has had a troubled taxonomic history. The name was originally proposed by Titus (1904) for *Robertsonella gleasoni* Titus, a new genus and species of megachilid bee from Grand Island, Illinois. For many years there was confusion as to identity of these bees since, while the males are fairly distinctive among osmiine megachilids, the females are not. Females of *Alcidamea*, another group previously given generic status but now also considered to be a subgenus of *Hoplitis*, were commonly misidentified as *Robertsonella*, leading to a misleadingly expansive distribution (Graenicher 1909; Hurd et al. 1980; Michener 1941, 1947; Pearson 1933) and some spurious host-parasite associations (Swenk 1914; Hurd 1979) for *Robertsonella*. In the first revision of *Robertsonella*, Michener (1938) found *Heriades simplex* Cresson to be a senior synonym of *R. gleasoni*. He also relegated *Robertsonella crataegina* Cockerell, a species described from Texas (Cockerell 1909), to subspecific status under *R. simplex*. Hurd and Michener (1955) later placed *Robertsonella* as a subgenus of *Hoplitis* stating that its primary distinguishing character, the near horizontal metanotum, did not outweigh its many similarities with *Hoplitis*. Later, the placement of *Robertsonella* in *Hoplitis* was strengthened by the discovery that *Robertsonella* shared the key synapomorphy of *Hoplitis*, the flap-like gradular projections of the male S6 (Griswold and Michener 1998; Michener 2007).

Species concepts in *Robertsonella* were greatly altered by Mitchell (1962). He described a new species, *Hoplitis (Robertsonella) micheneri* Mitchell, from Kansas and Georgia, resurrected *gleasoni* as a distinct species (with *crataegina* as a synonym), and described a new male that he associated with *H. simplex*. Although he separated the females of *gleasoni* and *simplex* in his key on the basis of their tergal punctation (close and coarse in *H. gleasoni*, finer and sparser in *H. simplex*), he stated in the text that the females of the two species could not be reliably separated. He went on to note that he might have erred when he associated his new male with *H. simplex*, a species previously known only as a female. A re-examination of the types of *H. simplex* and *H. gleasoni*, plus an analysis of the distribution of males, discussed below, involving more material than was available to Mitchell, indicates the sexes were indeed misassociated. A new species is described below for the male he incorrectly assigned to *H. simplex*.

A fourth species, *Robertsonella himachalli* Gupta was described from northwestern India in 1991, apparently under the erroneous impression that females of *Robertsonella* have an apico-median clypeal projection. If validly placed, this would be a remarkable range extension. Although I

have seen no specimens of this species, it is clear from the description and the characters used in the generic key (Gupta 1991, 1999) that this large (12 mm), metallic-blue species, the males of which have an apically emarginate T6 does not belong in *Robertsonella* and almost certainly is not a *Hoplitis*.

SYSTEMATICS

Hoplitis (Robertsonella) micheneri Mitchell

Hoplitis (Robertsonella) micheneri Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 65 (m, f)

Distribution.—USA: **Florida** (*Jackson, Suwannee*); **Georgia** (*Cobb, Fulton, Hamilton*): **Kansas** (*Douglas, Miami, Riley*); **Missouri** (*Shannon, Stoddard*); **North Carolina** (*Richmond*).

While sometimes locally abundant, (indicated by multiple collections from Suwannee Co., Florida), this bee appears to be rare with a possibly disjunct distribution. Populations are known from Kansas and Missouri and the southeastern U.S. (Florida, Georgia and North Carolina) (Fig. 1). Originally known only from Kansas and Georgia (Mitchell 1962), newer records from Missouri, North Carolina and Florida suggest additional fieldwork may eliminate the current disjunction in its distribution. Available floral records for females indicate it is specialist on *Amorpha fruticosa* (L.) (Fabaceae), a widespread shrub of the eastern U. S. It has repeatedly been collected on *A. fruticosa* in Kansas and Missouri and pollen analysis of the females from Florida collected at a nest site indicated scopal loads of nearly pure *A. fruticosa* pollen. Other floral records include *Rubus* (Rosaceae) and *Melilotus officinalis* (L.) Pall. (Fabaceae). *Hoplitis micheneri*, like other *Robertsonella*, is a vernal bee with flight records from 16 April (in Florida) to 13 June (in Missouri). Labels from a series of females from Suwannee River State Park, Florida collected by L. Stange stated they were "around small holes in old trees", suggesting this species utilizes small preexisting holes for its nests.

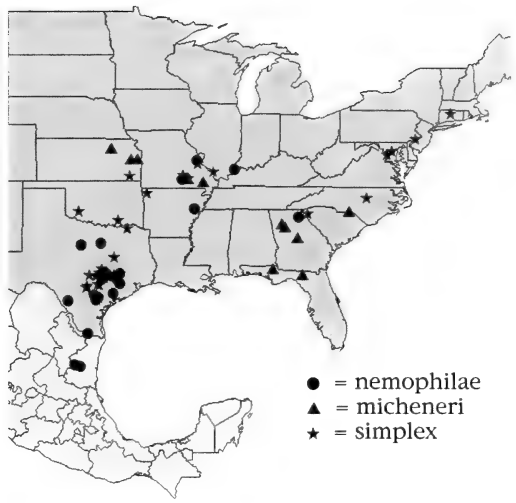


Fig. 1. Map of the distribution of *Hoplitis (Robertsonella)* spp. based on males.

Females are about the same size as *Hoplitis simplex* (HW = 2.19 ± 0.11 mm, 1.84–2.44, n=33; BL = 7.31 ± 0.52 mm, 6.16–8.48, n = 25) and are easily separated from other *Robertsonella* by having T1 shining with the punctures very fine and sparse. Males have the same pattern of facial pubescence as *H. nemophilae* but are about the same size as *H. simplex* (HW = 1.94 ± 0.05 mm, 1.79–2.20, n = 10 in *H. micheneri* vs. 1.92 ± 0.10 mm, 1.68–2.12, n = 66 in *H. simplex*). Males are distinctive in having S3 deeply emarginate (Fig. 5) [emargination of S3 very shallow and obscure in *H. nemophilae* and *H. simplex* (Fig. 4)].

Hoplitis (Robertsonella) simplex (Cresson)

Heriades simplex Cresson, 1864. Ent. Soc. Phila. Proc. 2, p. 384, f.

Robertsonella gleasoni Titus, 1904. N. Y. Ent. Soc. Jour. 12, p. 23, f, m.

Robertsonella crataegina Cockerell, 1909. Ann. Mag. Nat. Hist. (8) 4. 28.

Robertsonella simplex simplex: Michener, 1938. Ent. News 49, p. 131.

Robertsonella simplex crataegina: Michener, 1938. Ent. News 49, p. 130.

Hoplitis (Robertsonella) gleasoni: Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 65 (m, f in part)

Distribution.—USA: **Arkansas** (*Washington*); **Connecticut** (*Hartford*); **Illinois** (*Jackson*); **Kansas** (*LaBette*); **Missouri** (*Dent, Jefferson, Shannon*); **New Jersey** (*Camden*); **North Carolina** (*Wake*); **Oklahoma** (*Atoka, Kiowa*); **South Carolina** (*Anderson*); **Texas** (*Bastrop, Bee, Bexar, Blanco, Burleson, Goliad, Gonzalez, Grimes, Guadalupe, Karnes, Lamar, Lee, Limestone, Travis, Washington, Williamson*); **Virginia** (*Fairfax*).

Males of *Hoplitis gleasoni* and *H. simplex (sensu* Mitchell 1962) are easily separated by the characters in the key of Mitchell (1962). Males of *Hoplitis gleasoni* (*sensu* Mitchell 1962) occur from Connecticut and New Jersey to central Texas while males of *H. simplex* (*sensu* Mitchell 1962) are known from Indiana and North Carolina to central Tamaulipas (Fig. 1). As noted by Mitchell (1962), the female type of *H. simplex*, and females from the type series of *H. gleasoni* are not distinguishable so it is not obvious why the new male described by Mitchell was assigned to *H. simplex*. As the female type of *Hoplitis simplex* (Cresson) is from Connecticut but the nearest male of *H. simplex* (*sensu* Mitchell 1962) occurs some 1300 km away while a male of *H. gleasoni* (*sensu* Mitchell 1962 is known from Connecticut (Fig. 1) , it seems clear that the sexes were misassociated in Mitchell (1962). Thus, the original judgment of Michener (1938), that *H. gleasoni* is a junior synonym of *H. simplex*, is correct and *H. simplex* sensu Mitchell needs a new name that is provided below.

Males of *Hoplitis simplex* are easily distinguished from other *Robertsonella*, and all other North American osmiines, by the long mandibular fringe and the short, dense, appressed pubescence obscuring the clypeal surface. Females of *H. simplex* can be distinguished from *H. micheneri* by the characters listed above and in the key. Although females of *H. simplex* are, on average, slightly larger and more coarsely punctate than those of *H. nemophilae*, their size ranges overlap greatly, and, as the coarseness of the punctation varies with size, that character does as well.

Hoplitis simplex appears to be an oligolege of the Boraginaceae: Hydrophylloideae. The vast majority of floral records for females are for various *Nemophila* and *Phacelia* species. The only plants from which I have observed *H. simplex* females collecting pollen are *Nemophila phacelioides* Nutt., *N. sayersensis* Simpson *et al.*, *Phacelia congesta* Hook. and *P. strictiflora* (Engelm. & Gray) Gray in Texas (all Boraginaceae: Hydrophylloideae). Unfortunately, there are very few floral records for specimens from the northern part of its range. *Hoplitis simplex* is a vernal bee, active from mid March and April (in Texas) to late May (in Connecticut). A number of *simplex*-like females have been collected in Maryland in early June, but as no males were associated with these specimens, it is not clear if they are *H. simplex* or *H. nemophilae*.

The nest biology of *H. simplex* is described below.

Hoplitis (Robertsonella) nemophilae Neff, new species

Hoplitis (Robertsonella) simplex: Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 66. (m, f in part)

Diagnosis.—Males of *Hoplitis nemophilae* are distinguished from males of *H. simplex* by the longer, more erect clypeal pubescence, shorter mandibular fringe. They differ from *H. micheneri* by the weakly emarginate margin of S3 (strongly emarginate in *H. micheneri*). Females of *H. nemophilae* differ from those of *H. micheneri* by their denser punctation of T1 and lack the antero-median scutellar groove of that species. As noted above, females of *H. nemophilae* tend to be smaller and more finely punctate than those of *H. simplex*, but I know of no characters that consistently

distinguish females of *H. nemophilae* and *H. simplex*.

Description.—**Male:** Measurements: BL = 5.84 ± 0.32 mm, 5.04–6.65, n = 21; HW = 1.70 ± 0.08 mm, 1.54–1.84, n = 57. *Head*: Face approx. 1.2 × as broad as long, eyes convergent below (UIOD 1.4 × LIOD). Clypeus slightly convex, apical margin nearly straight, disc shining with fine, subcontiguous punctures. Supraclypeal area, parocular area, frons, vertex and gena finely, densely punctate. Labrum with apical margin weakly concave; basal width approx. 1.6 × length; apical width subequal to length; basal 1/3 to 1/2 smooth and shiny with very fine, very sparse punctures, punctures of distal half stronger, denser. Lateral ocelli closer to vertex than to eye (OC-O/OC-V = 1.5) with distance between lateral ocelli subequal to distance from lateral ocelli to eye. Scape slender, unmodified (scape length 2.8 times apical width); pedicel completely exposed; length flagellum (excluding pedicel) 5× scape length; flagellar segments (except first which tapers and is about as long as its apical width) slender, simple, about 1.5 × as long as wide. Gena about as wide as eye medially (in lateral view), tapering below. Hypostomal area shining, sparsely punctate. Mandible bidentate. Extended tongue length (glossa + prementum 2.0–2.2 mm, roughly 1.3 × head length). Ratio lengths labial palps: 3:6:1:1. Four maxillary palps, very short, fourth greatly reduced. *Thorax*: Scutum 2.9 × as long as scutellum, TTW = scutal length. Discs of scutum and scutellum shiny, with strong deep punctures approx 1–2 PW apart, scutellum densely punctate on posterior margin. Tegula shining, sparsely punctate. Metanotum dull, roughened, obscurely punctate. Propodeal triangle shining, impunctate, with narrow, shallowly, irregularly quadrately pitted apical area. Propodeal surfaces outside triangle roughened posteriorly, with shallow dense punctation more evident on anterior surfaces. Mesepisterum with strong dense punctures, punctures larger than on scutum. Legs normal. *Abdomen*: Terga shining, punctures fine, 1–3 PW apart, becoming slightly finer, denser towards distal margins. Terga 3–7 with narrow, impunctate distal margins, impunctate areas broadest on T6 and T7 which are slightly upturned, flange-like. T6 with minute lateral tooth, T7 rounded apically and with disc weakly depressed. S2 subconvex, most of apical margin straight, with dense, shallow punctation. Apical margin S3 very weakly emarginate medially, otherwise nearly straight, punctures as in S2 laterally but becoming very fine and dense medially. Margin S4 straight, punctures as in S2. Margin S5 straight but more rounded laterally, punctures as in S4. Margin S6 more convex but almost straight medially, surface smooth, nearly impunctate. S4–6 with narrow, translucent gradular flaps. S7, S8 and genital capsule as in figure 25 of *H. simplex sensu* Mitchell (Mitchell, 1962); gonocoxites with hairs of ventral surface erect, primarily in median portion. *Vestiture*: Hair all pale, sparse, erect except: clypeus with dense, erect to semi-erect, 0.32–0.35 mm long hairs with numerous short branches, hairs obscuring surface on apical 4/5 of clypeus; hair of supraclypeal area very short (0.04–0.08 mm), sub-appressed, sparse; hairs of parocular area and lateral areas of frons similar to those of clypeus but sparser, not obscuring surface; mandibular fringe weak, hairs 0.22–0.35 mm long, sparse ; T1-4 with narrow apical fascia of appressed, short hairs; fascia broadly interrupted on T1, more narrowly on T2, complete on T3-4, although often worn medially; discs of T1-7 with very sparse, very short, erect hairs; S3–5 with apical fringe of posteriorly oriented fine hairs (very weak medially on S2); S3 with apicomedial triangular patch of appressed hair in area of medial emargination, triangular patch of very short, very fine hairs basal to this. *Color*: Black except claws, distal tarsomeres, and apex of mandible reddish brown; tibial

spurs translucent yellow; wings lightly infuscated, nerves brown.

Female: BL = 6.61 ± 0.54 mm , n = 43, 5.60–7.36; HW = 1.77 ± 0.10 mm, n = 75, 1.48–1.96. *Head*: Face approx. 1.07 × as broad as long, eyes convergent below (UIOD 1.3 × LIOD). Clypeus similar to male but punctures shallow, 0.5 to 1 PW apart. Punctation of supraclypeal area, parocular area, frons, vertex and gena similar to male but slightly less dense. Labrum similar to male but basal width 1.2 × length; apical width slightly less (0.9 ×) than length; basal 1/5 shiny, impunctate, distal 4/5 punctate. Lateral ocellus closer to vertex than to eye (OCED/OCVD = 1.4) with distance between lateral ocelli subequal to distance from lateral ocellus to eye. Scape slender, unmodified (scape length 3.5 × apical width); pedicel completely exposed; length flagellum (excluding pedicle) 2.5 × length scape; first five flagellar segments slightly shorter than broad, gradually increasing in length and width distally, segments 6–9 as long as wide, segment 10 1.8 × as long as broad. Gena as in male. Hypostomal area shiny, impunctate. Mandible tridentate, middle tooth slightly nearer lower tooth than upper. Mouthparts as in male. *Thorax*: As in male. *Abdomen*: Terga shiny, punctation and surface sculpture as in male. T1-6 with distal margins very narrowly impunctate. T6 nearly straight in lateral profile, with apical margin very narrowly produced, shelf-like. *Vestiture*: Hair entirely pale, similar to male on head and thorax except sparse, semierect on clypeus and parocular areas, not obscuring surface; hypostomal area fringed laterally by long, erect, apically recurved hairs. T1-4 with narrow apical fascia of appressed, short hairs; fascia broadly interrupted on T1, very weak medially on T2 and entire on T3 & 4 (although often worn away); T6 with dense semi-appressed simple hairs giving disc whitish appearance. Scopal hairs simple, erect. *Color*: As in male.

Material examined.—Holotype ♂: USA, **Texas**, Hidalgo Co., Bentsen-Rio Grande State Park, 29-iii-1991, J. L. Neff K09033 , deposited KSEM. Allotype ♀: same data except K09128, collecting mud, deposited KSEM. Paratypes: MEXICO: **Tamaulipas**: 6 ♂, Guemez, Hcda. Santa Engracia, 11-iii-1991, J. L. Neff, on *Prosopis glandulosa*; 1 ♂, same data except on *Salix nigra*; 2 ♂, same data except *on Persea americana*; Llera: 2 ♂, Ciudad Victoria, 16 mi. S, 18-iii-1987, J. L. Neff, on *Prosopis glandulosa* (all CTMI);. USA: **Missouri**: Jefferson Co.: 1 ♂, 1 ♀, La Barque Creek Core Area, T43NR3ES32 to (SE4), Sandstone Glades, 6-7-v-2006, M. A. Arduser, ex yellow pan trap; Shannon Co.: 3 ♂, 1 ♀, Ozark N. Riverway, Round Spring Area, T30NR4W sect 19, 10-v-1990, M. Arduser, on flowers of *Phacelia*; 1 ♂, Chitter Creek Preserve by Cook Hollow, T28NR1WS21, 4-v-1998, M. Arduser, on flowers of *Phacelia* (all MSAC); **North Carolina**: (Raines Co.): 5 ♂, Bryson City, 23-iv-1923, J. C. Crawford, on *Fragaria virginiana*; 1 ♂, same data except 1-v-1923 on *Potentilla canadense* (all AMNH); **Texas**: Austin Co.: 1 ♂, Stephen F. Austin S. P., 9-iv-1966, J. C. Shafter (TAMU); Bastrop Co.: 2 ♂, Sayersville, 15-iv-1987, J. L. Neff on *Nemophila sayersensis* (CTMI);; 1 ♀, same data but 2-iv-1995 on *Nemophila sayersensis* (CTMI); 1 ♀, Stengl Lost Pines Biological Station, 3-iv-2008, J. L. Neff, on *Rubus trivialis* (CTMI); Bee Co.: 3 ♂, 4 ♀, Pettus, 3-iv-1988, J. L. Neff, on *Phacelia congesta* (CTMI); Brazos Co.: 3 ♂, College Station, Lick Creek Park, 7-17-1987, J. Heraty & Woolley, ex intercept/Malaise (TAMU); 3 ♀, 17-30-iv-1987, Woolley & Heraty, ex intercept/Malaise (TAMU); Burleson Co.: 3 ♂, 4 ♀, Burleson, 3 mi. N, J. L. Neff (CTMI), 8-iv-1986, on *Nemophila sayersensis*; Dimmit Co.: 6 ♂, 1 ♀, Carrizo Springs, 6 mi. E, 31-iii-1994, J. L. Neff and A. Hook (CTMI); Goliad Co.: 2 ♂, Charco, 1 mi. W, 18-iv-1987, J. L. Neff (CTMI), on *Nemophila phacelioides*; 1 ♀, same data but on *Phacelia congesta* (CTMI); Grimes Co.: 4 ♂, 2 ♀, Navasota, 2 mi. N, 6-iv-1988, J. L. Neff, on *Nemophila phacelioides* (CTMI); Hidalgo Co.: 1 ♂, same data as holotype (USNM); 23 ♀, same data as allotype (CTMI); 1 ♀, same data (USNM); 4 ♂, same data except 17-iii-1989 on *Lepidium virgatum* (CTMI); 7 ♂, same data except 17-iii-1989 on *Teucrium cubanense* (CTMI); 15 ♂; 1 ♀, same data except 16-iii-2007 (CTMI), on *Salix nigra*; 1 ♂, same data except 16-iii-2007 on *Ehretia anacua*

(CTMI); 7 ♂, 6 ♀same data except 19-iii-1992, A. W. Hook and C. R. Nelson (BFLC), no host; 2 ♂, same data except 15-iii-1982, C. Porter (FSCA); 3 ♂, same data except 16-iii-1982 (FSCA); 1 ♂, 1 ♀, same data except 17-iii-1982 (FSCA); 6 ♂, 1 ♀, same data except 23-iii-1984 (FSCA); 3 ♂, same data except 22-iii-1985 (FSCA); Karnes Co.: 1 ♂, Panna Maria, 1 mi. S, 18-iv-1987, J. L. Neff, on *Nemophila phacelioides* (CTMI); Lee Co.: 2 ♂, Fedor, 7-iv-1919, Birkmann (KSEM); 2 ♂, 1 ♀, Lexington, 1 mi. N, 8-iv-2005, J. L. Neff, on *Nemophila sayersensis* (CTMI); Washington Co.: 1 ♂, Washington, 3 mi. W, 8-iv-1987, J. L. Neff, on *Nemophila phacelioides* (CTMI); 1 male, Pickens Rd., 2.75 mi. N of rt. 105, 12-iii-2000, Panero, Crozier and Helfgott, on *Nemophila phacelioides* (CTMI); Zapata Co.: 1 ♀, San Ygnacio, 30-iii-1991, J. L. Neff and A. Hook, on *Phyla strigulosa* (CTMI); 1 ♀, San Ygnacio, 13 km N, (Arroyo Dolores), 2-iv-1994, A. W. Hook (BFLC). Other specimens: MEXICO: **Tamaulipas**: (Padilla), 12 ♂, 14 ♀, Rio Corona, 18 mi. N. of Ciudad Victoria, 1977, R. Schmidt (BLCU); USA: **Arkansas**: (St. Francis Co.), 2 ♂, Forest City, 11-iv-1946, C. D. Michener (KSEM); **Indiana**: Posey Co.: 2 ♂, Hovey Lake, Ent Recons. Station 12, 13-v-1958 (PURC); **Texas**: Colorado Co., 1 ♂, Columbus, 2-iv-1947, H. Townes (KSEM); Gonzalez Co.: 2 ♂, Luling, 30-iii-1951, R. H. Beamer, on *Salix* (KSEM); 1 ♂, same data (NCSU); 1 ♂, 2 ♀, Palmetto State Park, 5-iv-1954, R. E. Beer & party (KSEM); Hidalgo Co.: 1 ♂, Bentsen-Rio Grande S. P., 14-iii-1983 (BLCU), C. Porter; 1 ♂, same data except 15-iii-1983 (BLCU); 2 ♂, 1 ♀, same data except 17-iii-1983 (BLCU).

Discussion.—This species is described to include the males associated with *Hoplitis simplex* by Mitchell (1962). The justification for this is given in the discussion of *Hoplitis simplex*. Although broadly sympatric with *Hoplitis simplex* in the south-central United States, *H. nemophilae* has a more southerly distribution than *H. simplex*, ranging from southern Indiana to central Tamaulipas (Fig. 1). The name *nemophilae* refers to *Nemophila* (Boraginaceae: Hydrophylloideae), the flowers this species is mostly commonly associated with in central Texas. Despite the name, the species is probably not oligolectic on *Nemophila*, or even more generally oligolectic on the Hydrophylloideae. None of the collections from the southernmost portion of its range (southern Texas and Mexico) have been from *Nemophila* or other Hydrophylloideae. In fact, no *Nemophila* or *Phacelia* species were flowering in the vicinity of my collections of *H. nemophilae* in south Texas and Tamaulipas. The few pollen records from this area suggest that *Prosopis* (Fabaceae) and *Rubus* (Rosaceae) are pollen hosts in the absence of Hydrophylloideae. Females were also observed at male catkins of *Salix nigra* Marsh. in south Texas, although none bore scopal pollen loads. Like other *Robertsonella*, *Hoplitis nemophilae* is a vernal species, active from mid March through mid April (in Texas) but as late as early June in the northern part of its range (Indiana).

Nests are unknown but numerous females of *Hoplitis nemophilae* were observed gathering mud at communal mud-gathering sites on the banks of resacas (oxbow lakes), wildlife watering areas and the Rio Grande at Bentsen-Rio Grande State Park, Hidalgo Co., Texas indicating that it, like *H. simplex*, uses mud for nest construction.

KEY

MALES

1. Clypeal pubescence of very short (0.08–0.10 mm), branched, dense, appressed hairs, hairs particularly dense on apical half; mandibular fringe of hairs on lower margin of mandibles long (max. length 0.53–0.65 mm) and dense (Fig. 2); S3 with a very shallow, median emargination, area of emargination with triangular patch of semi-appressed setae (Fig. 4); mandibles broad basally, basal width 0.4 × eye length . . . . . ***H. simplex* (Cresson)**

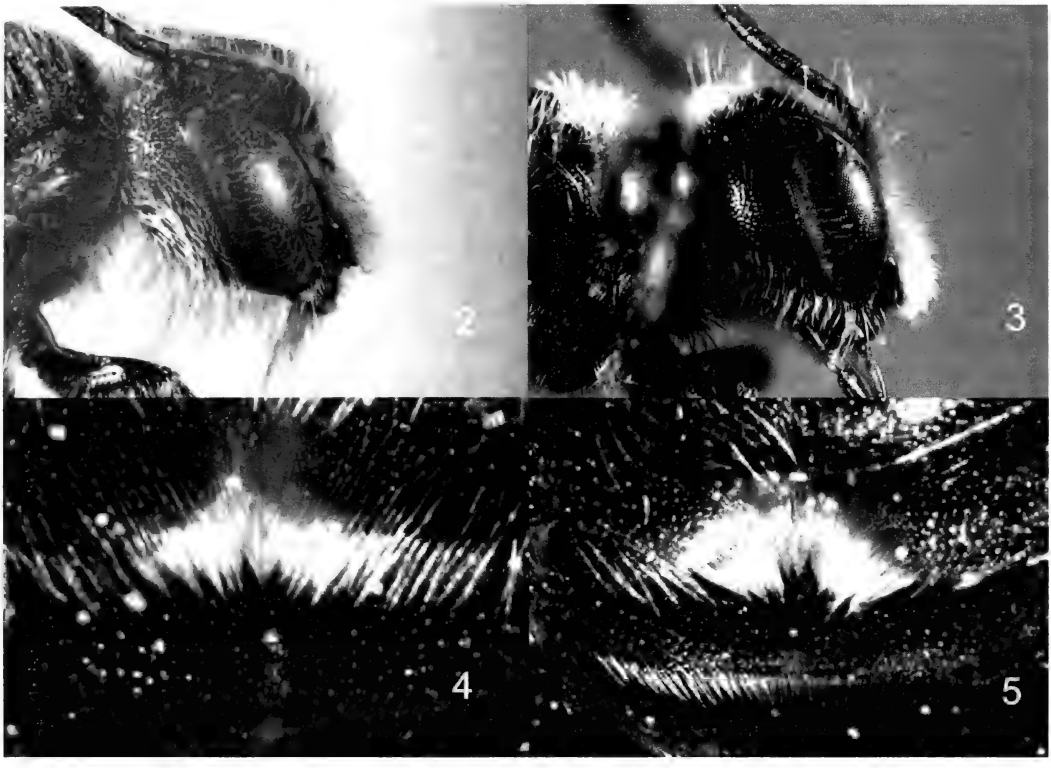


Fig. 2. Head of *Hoplitis simplex* male, lateral view.
Fig. 3. Head of *Hoplitis nemophilae* male, lateral view.
Fig. 4. S3 of *Hoplitis nemophilae* male.
Fig. 5. S3 of *Hoplitis micheneri*, male.

1a. Clypeal pubescence longer (0.32–0.36 mm), erect to suberect; mandibular fringe short (max. length 0.22–0.35 mm) and thin (Fig. 3); S3 variable; base of mandible narrower, basal width narrower, 0.3 × eye length 2

2. Apical margin of S3 nearly straight, emargination very weak, area of emargination with triangular patch of semi-appressed white hair (Fig. 4) . . . . ***H. nemophilae*** **Neff**

2a. Apical margin of S3 deeply emarginate, emargination approximately ¼ as broad as sternum and lined with a dense fringe of long white hair (Fig. 5) . . . . . ***H. micheneri*** **Mitchell**

FEMALES

1. Punctation of T1 very fine and sparse, punctures 4+ PW apart on disc; scutellum with narrow, impunctate antero-median depression . . . . . ***H. micheneri*** **Mitchell**

2. Punctation of T1 fine and deep, punctures 2–3 PW apart on disc, scutellum uniformly punctate . . . . . ***H. nemophilae*** **Neff** or ***H. simplex*** **(Cresson)***

* males of *nemophilae* and *simplex* cannot be reliably separated without associated males.

BIOLOGY OF *HOPLITIS SIMPLEX*

Nests and nest construction.—Hoplitis simplex is a cavity renting species. There is no evidence it ever excavates its own burrows in pithy stems like some other *Hoplitis* (Rau 1928; Michener 1955). Natural nests have been observed in small diameter beetle galleries in tree branches and stems. *Hoplitis simplex* females also readily accept trap nests bored in pine blocks. Trap nest diameters utilized by *H. simplex* ranged from 2.8 to 4.8 mm. Larger diameter nests were present but not utilized by *H. simplex*. The diameter most frequently occupied by *H. simplex* was 3.2 mm during my observations but the nest arrays were not appropriate for determining nest size preferences. Reuse of nests, either of old *H. simplex* nests, or those of various mud-using eumenine wasps, was common.

Nests plugs, partitions, and sometimes wall linings, are constructed only of fine soil, without any added pebbles or vegetable material. Females have repeatedly been observed collecting mud at communal mud gathering areas at the edge of streams, seeps or ponds (Fig. 7). Numerous females repeatedly visited communal sites on the edge of streams or seeps to gather fine-grained mud. Such areas take on a honeycombed appearance from the many small tunnels and pits excavated by the mud collecting bees. This mud is held beneath the mandibles as a pellet on the smooth, hairless surfaces of the hypostomal area, a corbicula-like area fringed laterally by long curved hairs. In the absence of appropriate mud sources, *H. simplex* may create its own mud by adding fluids, probably regurgitated nectar, to dry soil. A single female was observed doing so near Sayersville, Bastrop Co., Texas. Many of the soil-gathering trips (discussed below) timed at BFL seemed to be too brief to allow for flight to distant mud sites. Moreover, tests of the partitions proved positive for sucrose, although this could have been contamination from the provisions or added later while the bee was working in the nest.

Nest architecture varies with the relationship of bee body diameter and nest diameter. When bee body diameter and nest diameter are similar, nests are simple linear arrays of cells separated by soil closed with an outer mud plug. Occasionally, when the cross-sectional diameter of the bee is significantly smaller than the diameter of the cavity she is using (such as in 4.8 mm diameter trap nests), she may line the cell walls with mud to create cells whose diameter more closely matches her own. In 60% of the measured nests, the posterior end of the nest was indicated by a relatively thin (1.4 ± 1.3 mm, n = 7) soil partition. In borings less than 50 mm long, this was almost always flush with the end of the boring, but in longer holes this final partition often was placed some distance in front of the end of the boring. Vestibular cells (length = 15.0 ± 9.0 mm, 5.1–42.0, n = 18) were present in 58.3% of the nests. Eighty percent of the nests in 100 mm long borings had vestibular cells compared to only 50% of the nests in borings less than 50 mm long. In addition to the vestibular cells, short intercalary cells were observed in 5% (2 of 38) of the nests. The number of cells per nest averaged 7.9 ± 2.1 (n = 10, 5–11) in 100 mm long borings and 2.5 ± 1.0 (n = 26, 1–4) for borings less than 50 mm. Cell length averaged 9.0 ± 2.3 mm (n = 73, 5.2–19.7). No position-specific significant differences were found between lengths of cells within the nests. The cell partitions are concave on their anterior surface, flat posteriorly, rather thin medially (0.5 ± 0.1 mm, n = 8, 0.4–0.6) and wider on the cell walls (1.4 ± 0.7 mm, n = 7, 0.5–2.3). The cell plug was rather short (4.0 ± 1.5 mm, n =27, 1.2–7.5) and flush with the entrance in 39.4% of the nests. In the remaining nests it was slightly recessed (2.5 ± 1.4 mm, n = 9, 1.0–4.2) from the entrance.

Females averaged 2.70 ± 2.33 min per trip (0.03–24.35, n = 388) for soil collecting

trips and spent an average of 2.07 ± 2.68 min (0.03–25.00, n = 380) in the nest constructing cell partitions or nest plugs. Time spent gathering mud at communal sites averaged 21.8 ± 6.1 sec (12.7–37.5, n = 30). It took an average of 10.7 ± 5.0 soil gathering trips (5–24, n = 12) to construct a partition in a 3.2 mm diameter nest, 12.5 ± 2.9 (8–16, n = 6) for 4.0 mm nests and 10 trips (n = 2) for 4.8 mm nests. Usually only two trips were required to close a cell and the remaining trips were for adding additional soil to the partition or cell walls. Time to construct a partition in a 3.2 mm diameter nest averaged 52.27 ± 26.08 min (24.00–106.97, n = 12), 80.35 ± 27.38 min (57–117, n = 6) in 4.0 mm nests and 52.00 ± 11.31 min (44.00–60.00 min, n = 2) for 4.8 mm nests. Times and number of trips for constructing partitions in the 4.8 mm nests are not strictly comparable to those for the 3.2 and 4.0 mm nests because the former had previously been occupied by eumenine wasps and had pre-existing partial partitions, while the latter nests were previously unoccupied. Nest closure (sometimes the closure for the last cell plus the cell plug when a vestibular cell was present) required an average 22.67 ± 5.61 trips (14–34, n = 9) for 3.2 mm nests, 22 trips (n = 1) for 4.0 mm nests and 34 trips (n = 1) for 4.8 mm nests. Time to complete the closure averaged 83.07 ± 25.59 min (43.9–148.77, n = 9) for 3.2 mm nests, 123.67 min (n = 1) for 4.0 mm nests and 127.1 min (n = 1) for 4.8 mm nests. The basal partition of a 3.2 mm nest was accurately timed only once and required 2 trips and 14 min.

Intrafloral behavior.—Visits to flowers of *Nemophila phacelioides*, the primary host of *Hoplitis simplex* at BFL, are typically brief. Females foraging at midday on flowers of *N. phacelioides* at BFL averaged 5.5 ± 4.1 sec (n = 50, 0.9–19.6) for nectar and pollen collecting visits and 4.8 ± 2.9 sec (n = 15, 0.9 = 9.4) for nectar only visits. The pale blue flowers of *N. phacelioides* have rotate corollas with five erect stamens and five nectaries. The nectaries are located between the anther bases and are hidden by scales. Females of *H. simplex* are able to simultaneously forage for pollen and nectar by perching on individual anthers (Fig. 8). A female scrapes pollen directly from the anthers into her abdominal scopa using her hind legs while tapping the anthers with her abdomen. At the same time, she inserts her mouthparts into the nectary below. Unlike females of *Andrena sagittagalea* Ribble, another bee common on *Nemophila* in central Texas, *H. simplex* females do not vibrate or buzz the anthers of *N. phacelioides* while harvesting pollen.

Hoplitis simplex is not an early foraging bee, at least at BFL. Foraging by females usually begins after 1000 AM, a time that corresponds with the usual initiation of nectar production in *N. phacelioides* flowers at BFL. Pollen availability from *N. phacelioides* continues through the day as anther dehiscence and floral anthesis occurs asynchronously; foraging continues until near dusk.

Provisioning.—Females of *Hoplitis simplex* are able to construct and provision up to three cells per day, although typically they complete only one or two. On average it took 10.8 ± 1.8 (7–15, n = 27) pollen trips to provision a cell. The distribution of pollen trips per cell was unimodal (mode of 10) with 85.2% of the provisioning series entailing 9–12 pollen trips. The mean duration of a pollen collecting trip was 8.38 ± 4.59 min (1.50–33.02, n = 320). For individual cell provisioning series, the mean duration of a pollen collecting trip ranged from 3.21 to 17.50 min with mean trip duration decreasing through the day (Mean Trip Duration = 28.222–1.506 × Start Time, r^2 =0.468, F = 0.0003). Time to provision a cell (including time in the nest) averaged 114.11 ± 40.02 min (61.00–192.60, n = 27). Although the correlation is weaker, provisioning time per cell also decreased through the day (Provisioning Duration per Cell = 280.05–12.402 × Start Time, r^2 = .262, F = 0 .0063

Females averaged 2.49 ± 3.48 min (0.14–46.78, n = 313) in the nest between provisioning trips. As in many other megachilid bees, females typically would deposit nectar into the provision mass, working it with her mandibles, then, if the nest was too narrow to permit turning around within the nest, back out of the nest, turn around and back in to deposit pollen. The initial nectar deposition phase averaged 0.85 ± 0. 41 min (0.08–3.50, n = 285) and pollen deposition averaged 1.54 ± 3.03 min (0.17–46.28, n = 254). After the last pollen trip of a provisioning series, the female usually made a short final trip, presumably for nectar, averaging 1.90 ± 2.14 min (0.08–9.28, n = 26). Upon returning from this last trip, she spent 1.35 ± 0.96 min (0.48–5.47, n = 26) in the nest depositing nectar. She then turned around, backed in and spent 1.14 ± 0.60 min (0.38–3.15, n = 29) in the nest, during which time oviposition occurred.

Development and cocoon construction.— The slightly wider posterior end (0.6 mm vs. 0 5 mm anteriorly) of the slightly curved, 2 mm long egg is inserted into the slanting upper face of the provisions (Fig. 6). Eclosion occurs 3–4 days after oviposition. The first evident instar (presumably the second larval instar since in most LT bees the first molt occurs within the chorion (Torchio 1989, Trostle and Torchio 1994)) bends downwards and begins feeding within a few hours of eclosion. This instar has a HW of 0.40 mm. If we start the development clock as day 0 at eclosion, the molt to the third larval instar (with a HW of 0.48 mm) occurs on day 2, the molt to the fourth larval instar (HW = 0.60 mm) occurs on day 4 and the final larval molt to the fifth instar (HW = 0.70 mm) on day 6 or 7. Throughout this initial period, the glabrous larva feeds while remaining attached to the provision mass at the original place of insertion of the egg, gradually excavating an antero-ventral cavity in the provision mass. The fifth larval instar, easily recognizable by its setose integument, initially remains attached to the place of egg insertion, continues feeding, and begins defecating the day after the fourth molt (day 7 or 8). Fecal pellets are pale yellow, smooth, slightly arched, truncate cylinders averaging 0.44 ± 0.11 mm long (0.70–0.10, n = 30) and 0.22 ± 0.02 mm in diameter (0.24–0.18, n = 30). It continues feeding and defecating while attached to the provision mass for another three or four days (days 10–12) before releasing itself and beginning to move over the remaining provision mass. The larva continues moving, feeding and defecating for another three to four days. On day 13–16, in addition to the previously mentioned activities, the larva begins to construct the operimentum (Mathews 1965), a translucent, secreted lining adhering closely to the anterior partition and adjacent walls of the cell (Fig. 9). Intermittent feeding and operimentum construction continues for another 10 days or so (to days 23–26) until a strong lining has built up on the anterior portion of the cell walls, and the provisions are consumed (or nearly so). The larva then begins cocoon construction by spinning a delicate collar or hood-like structure attached to the edges of the anterior cell partition and slanting posteriorly to what will become the anterior portion of the cocoon (Fig. 9). Since the collar occupies the space between the anterior end of the cocoon and the anterior cell partition, its length varies with cell and cocoon size. In relatively short cells (7 mm or less) it may be little more than a rim of silk connecting the cocoon to the operimentum. Usually, most of the feces are loosely contained between the sides of collar and the cell walls, although in some, nearly all is trapped between the sides of cocoon and the cell walls. Upon completing this structure, the larva begins working on the cocoon walls, creating a tough, single layered, translucent, cylindrical structure with a rounded anterior end. The cocoon usually contacts the cell walls laterally and

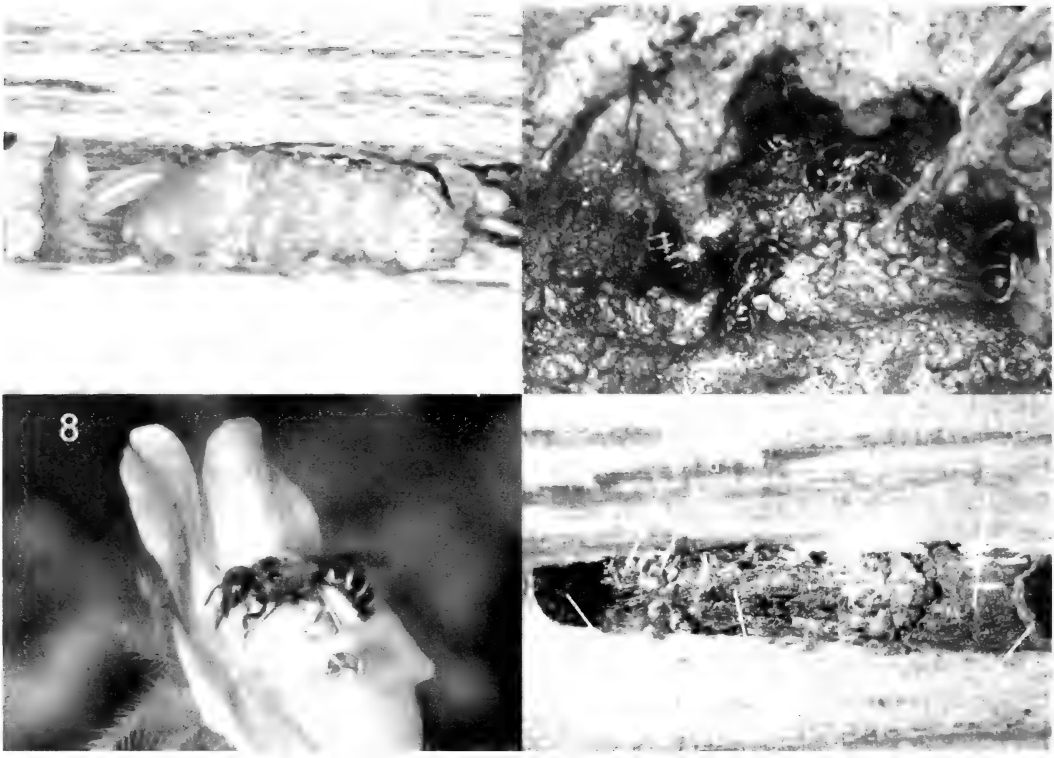


Fig. 6. *Hoplitis simplex* provision mass with egg.
Fig. 7. *Hoplitis simplex* females at mud collection site.
Fig. 8. *Hoplitis simplex* female foraging for nectar and pollen on flower of *Nemophila phacelioides*.
Fig. 9. Cocoon of *Hoplitis simplex*: a - operimentum; b - collar (torn); c - cocoon proper; d - fecal pellets; e - cell partition.

lacks an obvious nipple or anterior thickening. The precise shape of the cocoon depends on whether or not its posterior end contacts the posterior cell partition, conforming to shape of the partition if it does, and more oval if it does not. Cocoon construction requires five to six days. Upon completing the cocoon, the larva enters a dormant state, in which it remains until the following spring, when it pupates and emerges from the nest.

Emergence and sex ratio.—Hoplitis simplex is clearly protandrous. 1988 emergence from a set of nests maintained under ambient conditions and provisioned in 1987 occurred over 7 days (1–7 April) with 81.6% (31 of 38) of the males emerging in the first 3 days before the first female emerged. The overall sex ratio was 2.92 M: F. In 1989, bees from nests provisioned in 1988 emerged over a 15 day period, interrupted by a 6 day cold spell when daily highs did not exceed 15° C and no emergence occurred. Again, 91.2% (52 of 57) males emerged in the first four days of emergence, while only 7.1% (3 of 42) females did so during the same period. The 1989 sex ratio was 1. 35 M: F and the combined 1988+1989 sex ratio was 1.72. An average male of *H. simplex* from BFL was lighter (dry weight = 4.4 ± 0.7 mg, n = 7, 3.6–5.4) than the average female (6.5 ± 1.1 mg, n = 23, 3.2–8.4), even though the smallest female was lighter than the smallest male. If, as is commonly assumed, investment is proportional to dry mass, then the expected M:F sex ratio based on adult dry weights would be 1.48:1. This is close to the observed 1989 ratio but quite different from that in 1988. The available

data are inadequate to resolve this discrepancy.

Males and mating.—Male *Hoplitis simplex* patrol and forage at flowers utilized by the females. They were not observed patrolling nest sites, emergence sites or mud collecting areas. The few observations of mating suggest it is very perfunctory. A patrolling male would pounce on a female when she landed on a flower. This was followed by a brief period of copulation with the male leaving without any mate guarding or post-copulatory mating display.

Parasites and predators.—Females of a small, undescribed *Stelis* sp. (F. Parker, pers. com.) were repeatedly observed at the entrances of *Hoplitis simplex* nests at BFL and occasionally entering the nests. In one dissected nest, the *Stelis* egg was placed at the rear of the cell and the hairy, motile last larval instar was the hospicidal form that killed the host. Several males and females of the undescribed *Stelis* were reared from *H. simplex* nests and others were detected in nest dissections by their distinctive nippled cocoons and dark fecal pellets. The report of *Stelis lateralis* being reared from a *Hoplitis simplex* nest from Nebraska (Hurd 1979, Swenk 1914) is almost certainly based on a misidentified *Alcidamea* nest as I know of no valid records for *Robertsonella* from this area.

The outermost cells of some completed nests of *Hoplitis simplex* at BFL were occasionally destroyed by raiding fire ants (*Solenopsis invicta* Buren), although they rarely destroyed the inner cells.

DISCUSSION

The nesting biology of the Osmiini is famously diverse with some species excavating nests in the soil, others excavating nests in pithy stems, many using pre-existing cavities and some constructing free standing mortar nests (Michener 2007). Materials used in nest construction include various combinations of resin, pebbles, soil, masticated leaves, petals and wood chips (Michener 2007). Cavity nesting appears to be plesiomorphic in the Osmiini as it is widespread, perhaps universal, in the basal *Chelostoma* and heriadine lineages (Michener 2007; Praz et al. 2008), but it may be secondarily derived in *Hoplitis* where nests excavated in soil are common in several basal lineages (Praz et al. 2008). The nests of *Hoplitis simplex* (and probably other *Robertsonella*), constructed in pre-existing cavities with mud, without any pebbles or plant material or other amendments, appear to be unique in *Hoplitis* (the vast majority of whose reported nests are constructed with masticated plant parts, often with additional materials) and unusual in the Osmiini (Michener 2007), found elsewhere only in *Chelostoma* (Parker 1988) and some *Osmia* species (Bosch et al. 2001; Cane et al. 2007). The use of soil for nest construction by *Robertsonella* appears to be derived within *Hoplitis* but this will require more data on the nests of other *Hoplitis* taxa and a better understanding of the phylogenetic position of *Robertsonella*. Our understanding of the phylogeny of *Hoplitis* has recently been greatly enhanced by a molecular analysis of the Osmiini (Praz et al. 2008) which included representatives of 18 of the 27 subgenera of *Hoplitis* recognized by Michener (2007). Unfortunately, *Robertsonella* was not one of the included subgenera.

The distinctive cocoons of *Hoplitis simplex*, with the operimentum, collar and nipple-less, single layered, inner cocoon appear to be quite similar to those reported for *H. (Cyrtosmia) hypocrita* (Cockerell), *H. (Monumetha) fulgida* (Cresson) and *H. (Alcidamea) sambuci* Titus (Clement and Rust 1976). The inner cocoons of *H. hypocrita* and *H. fulgida* differ from those of *H. simplex* in having nipples, and all three differ in that the collar connecting the operimentum (the collar of Clement and Rust 1976) to the inner cocoon is a network of threads, rather than the mixture of threads and sheet-like material in the collar of *H. simplex*. The cocoons of members of *Acrosmia* (Parker 1978), *Dasyosmia* (Rust 1980), *Formicapis*

(Rust and Clement 1975), *Hoplitis s. str.* (Eickwort 1973), and the *Proteriades* group (*Hoplitina*, *Penteriades* and *Proteriades*) (Parker 1978) all lack an operimentum or a collar. The outer cocoons of this latter group of taxa may be homologous with the operimentum, but at least in *H. (Hoplitis) anthocopoides* (Schenck), it is spun after the completion of feeding (Eickwort 1973), rather than shortly after the fifth molt as in *H. simplex*. Using the molecular analysis of Praz et al. (2008) as a framework, cocoon structure suggests that *Robertsonella* will be found to be more closely related to the clade including *Alcidamea*, *Cyrtosmia* and *Monumetha*, than the larger, mainly old world clade including *Formicapis* and the *Proteriades* group.

There are very few data available on the foraging behavior of other *Hoplitis* species. A notable exception is the report of Strickler (1979) on *H. (Hoplitis) anthocopoides* (Schenck), a specialist on *Echium* (Boraginaceae). She found that *H. anthocopoides* collected about the same amount of pollen per visit as individuals of several similarly sized generalist bee species, but it spent much less time per flower and less time moving between flowers and stalks of its preferred host than did the generalists. She noted that the increased foraging speed might require increased energy expenditure, and hence increased time spent foraging for nectar. However, in the case of *H. anthocopoides*, increased time costs would be minimal since it harvests nectar and pollen simultaneously. This advantage probably also applies to *H. simplex* since it also simultaneously harvests pollen and nectar.

In *Robertsonella*, *Hoplitis micheneri* appears to be is an oligolege of *Amorpha*, *H. simplex* appears to be oligolectic on the Hydrophylloideae and *H. nemophilae* is polylectic with a strong preference for the Hydrophylloideae. The status of *H. simplex* as oligolectic is tentative since there are very few floral records from the northern part of its range. With more data, it may prove to be like polylectic like *H. nemophilae*, again with a strong preference for the Hydrophylloideae. Interestingly, no *H. micheneri* have been reported visiting any Hydrophylloideae while no *H. simplex* or *H. nemophilae* have been reported visiting *Amorpha*, although both plant groups are widespread and occur in the ranges of all three bee species. Phylogenetically distant, the flowers of both groups do share the characters of short, exserted anthers. Females of *H. simplex* and *H. nemophilae* are able to perch on *Nemophila* and *Phacelia* anthers and simultaneously collect pollen and nectar. Foraging behavior of *H. micheneri* has not been reported but I expect similar behavior on the flowers of *Amorpha*, which are superficially similar to *Phacelia* flowers. Flowers of *Prosopis* and *Salix*, suspected floral hosts of *H. nemophilae*, share the same morphology.

At 10.8 trips per cell, *Hoplitis simplex* falls very close to the mean number of trips per female cell for all bees ($x = 11.66 \pm 8.84$, $n = 72$, 2–40, median = 9.25, data set of Neff (2008)). However, it is more than the mean number of trips per cell for other small (body dry weight < 10 mg) bees ($x = 6.13 \pm 3.40$, $n = 27$, 2–17, median = 5.0). Although the data set is too small for firm conclusions, megachilids have a higher mean number of trips per cell ($x = 23.24 \pm 10.66$, $n = 15$, 10–40, median = 17.60) versus that of all other bees ($x = 8.76 \pm 5.11$, $n = 57$, 2–22, median = 8.00). This high number of trips suggests that either megachilids require more pollen per cell than other bees, or more likely, their ventral scopae have a smaller pollen transport capacity than bees with other means of external pollen transport.

ACKNOWLEDGMENTS

This paper is dedicated to Roy Snelling, who was a source of inspiration during my ongoing education about bees. I thank Larry Gilbert for permission for field work at BFL and the Texas Parks and Wildlife Department for permits for studies in Texas State Parks. The curators of the following collections generously lent material or allowed me to examine

material in their collections: Academy of Natural Sciences (Philadelphia), American Museum of Natural History (New York), Smithsonian Institution (Washington, D. C.), University of Kansas (Lawrence), Florida State University (Tallahassee), Purdue University (Purdue), Texas A & M University (College Station), University of Texas (Austin), North Carolina State University (Raleigh), University of Missouri-Columbia; Lousiana State University (Baton Rouge), U.S. National Pollinating Insects Collection (Logan) and the M. Arduser Collection (Missouri). I also thank Kendra Bauer for preparing the map and Ulrich Müller and Sze Huei Yek for access to, and assistance with, the Photomontagey system.

LITERATURE CITED

Bosch, J., Y. Maeta, and R. Rust. 2001. A phylogenetic analysis of nesting behavior in the genus *Osmia* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* 94: 617–27.

Cane, J. H., T. Griswold, and F. D. Parker. 2007. Substrates and materials used for nesting by North American Osmia bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* 100: 350–58.

Clement, S. L. and R. W. Rust. 1975. The biology of *Hoplitis robusta* (Hymenoptera: Megachilidae). *Entomological News* 86: 115–20.

———. 1976. The nesting biology of three species of *Hoplitis* Klug. *Pan-Pacific Entomologist* 52: 110–19.

Cockerell, T. D. A. 1909. Descriptions and records of bees. -XXI. *Annals and Magazine of Natural History, ser. 8* 4: 25–31.

Cresson, E. T. 1864. On the North American species of several genera of Apidae. *Proceedings of the Entomological Society of Philadelphia* 2: 373–411.

Eickwort, G. C. 1973. Biology of the European mason bee, *Hoplitis anthocopoides* (Hymenoptera: Megachilidae) in New York state. *Search: Agriculture* 3: 1–32.

Graenicher, S. 1909. Wisconsin Flowers and their pollination: Compositae, Part I. *Bulletin of the Wisconsin Natural History Society* 7: 19–77.

Griswold, T. L. and C. D. Michener. 1998. The classification of the Osmiini of the Eastern Hemisphere (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society* 70: 207–53.

Gupta, R. K. 1991. On genus *Robertsonella* Titus, with a description of a new species from Himachal Pradesh, India (Insecta, Hymenoptera, Apoidea - Megachilidae). *Reichenbachia* 28: 173–75.

———. 1999. *Taxonomic Studies on the Megachilidae of North-Western India*. Scientific Publishers (India), Jodhpur. 291 pp.

Hurd, P. D. Jr., W. E. LaBerge, and E. G. Linsley. 1980. Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 310: 158 pp.

———. 1979. Superfamily Apoidea. Pp. 1741–2209 *in* Krombein, K. V., P. D. Hurd, Jr, D. R. Smith, and B. D. Burks, eds. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, D. C.

——— and C. D. Michener. 1955. The megachiline bees of California (Hymenoptera: Megachilidae). *Bulletin of the California Insect Survey* 3: 1–247.

Matthews, R. W. 1965. The biology of *Heriades carinata* Cresson (Hymenoptera, Megachilidae). *Contributions of the American Entomological Institute* 1: 1–33.

Michener, C. D. 1938. The bees of the genera *Chelostomopsis, Formicapis, Robertsonella*, and *Prochelostoma* (Hymen.: Megachilidae). *Entomological News* 49: 127–32.

———. 1941. A generic revision of the American Osmiinae with descriptive notes on Old World genera (Hymenoptera: Megachilidae). *American Midland Naturalist* 26: 147–76.

———. 1947. A revision of the American species of *Hoplitis* (Hymenoptera, Megachilidae). *Bulletin of the American Museum of Natural History* 89: 257–318.

———. 1955. Some biological observations on *Hoplitis pilosifrons* and *Stelis lateralis* (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society* 28: 81–87.

———. 2007. *The Bees of the World*. The Johns Hopkins University Press, Baltimore. xvi + 953 pp.

Mitchell, T. B. 1962. Bees of the Eastern United States, Volume II. *North Carolina Agricultural Station Technical Bulletin* 152: 1–557.

Neff, J. L. 2004. Hooked hairs and not so narrow tubes: two new species of *Colletes* Latreille from Texas (Hymenoptera: Apoidea: Colletidae). *Journal of Hymenoptera Research* 13: 250–261.

———. 2008. Components of nest provisioning behavior in solitary bees (Hymenoptera: Apoidea). *Apidologie* 39: 30–45.

Parker, F. D. 1978. Biology of the bee genus *Proteriades* Titus (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 51: 145–73.

———. 1988. Nesting biology of two North American species of *Chelostoma* (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist* 64: 1–8.

Pearson, J. F. W. 1933. Studies on the ecological relations of bees in the Chicago region. *Ecological Monographs* 3: 373–441.

Praz, C. J., A. Müller, B. N. Danforth, T. L. Griswold, A. Widmer, and S. Dorn. 2008. Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). *Molecular Phylogenetics and Evolution* 49: 185–97.

Rau, P. 1928. The nesting habits of the pulp-making bee, *Alcidamea producta* Cress. *Psyche* 100–07.

Rust, R. W. 1980. Nesting biology of *Hoplitis biscutellae* (Cockerell) (Hymenoptera: Megachilidae). *Entomological News* 91: 105–09.

Strickler, K. S. 1979. Specialization and foraging efficiency of solitary bees. *Ecology* 60: 998–1009.

Swenk, M. H. 1914. I. Studies of the North American bees. II. Family Stelididae. *Nebraska University Studies* 14: 1–36.

Titus, E. S. G. 1904. Notes on Osmiinae with description of new genera and species. *Journal of the New York Entomological Society* 12: 22–27.

Torchio, P. F. 1989. In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* 82: 599–615.

Trostle, G. and P. F. Torchio. 1994. Comparative nesting behavior and immature development of *Megachile rotundata* (Fabricius) and *Megachile apicalis* Spinola (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 67: 53–72.

J. HYM. RES.
Vol. 18(2), 2009, pp. 167–174

The Mating System and Prey Selection in the Digger Wasp *Aphilanthops hispidus* W. Fox (Hymenoptera: Crabronidae)

JOHN ALCOCK

School of Life Sciences, Arizona State University, Tempe AZ 85287-4501

Abstract.—The mating system of the digger wasp *Aphilanthops hispidus* W. Fox at a site in central Arizona is one in which males patrol the edges of a large nesting/emergence area in a narrow dry watercourse and also around one or more flowering shrubs of catclaw acacia. Patrolling males sometimes pounce on unreceptive females that they encounter in their flight paths suggesting that they may be seeking recently emerged virgin females. After mating, females build nest burrows in the dry wash. They stock their nests primarily with small native bees belonging to five different families. The introduced honey bee, *Apis mellifera*, is however the single most frequently taken prey species. That females of *A. hispidus* also take the occasional wasp demonstrates that they are generalist predators unlike their close relatives, which specialize in the capture of *Formica* ants.

Although widespread in the southwestern United States and northern Mexico, little is known about the digger wasp *Aphilanthops hispidus* W. Fox. Indeed, nothing has been written on the wasp's behavior other than a short note (Evans 1977) that listed the bees taken as prey by one female of the species. Some other members of the genus are known to prey exclusively on ants (Bohart 1966). In addition, the territorial mating system of *A. subfrigidus* has been described in some detail (O'Neill 1990). Here I report on the natural history of *A. hispidus*, a common species in desert habitat near Phoenix, Arizona. The focus of the paper will be on how males attempt to acquire mates and on the identity of the prey species taken by nesting females.

METHODS

Observations on the behavior of male and female *A. hispidus* were made at a desert site about 4 km north of the intersection of East McDowell Road with Power Road (which then becomes the Bush Highway). The site features a dry wash; the wasps were studied at a location about 1 km up the wash to the east of Bush Highway where the sand and fine gravel bed was only 4 to 6 m wide (Fig. 1). The wash was bordered primarily by creosote bush (*Larrea tridentata* (DC.) Coville), the dominant plant in the area, with occasional foothills paloverdes (*Parkinsonia microphylla* Torr.), ironwood trees (*Olneya tesota* A. Gray), catclaw acacia (*Acacia greggii* A. Gray), and buckhorn cholla cactus (*Opuntia acanthocarpa* (Engelm. & Bigelow) F.M. Knuth).

The wasps were studied over four years: in 2006, from 24 April to 11 May for a total of 9 days; in 2007, from 29 April to 4 May for a total of 4 days; in 2008, from 21 April to 2 May for a total of 5 days; and in 2009, from 7 April to 7 May for a total of 17 days. On any given day, the study site was visited from 1 to 4 h beginning at various times from mid-morning to late afternoon. During the observer's visits, any females that were seen carrying prey and about to enter their nests, many of which were located in a section of wash approximately 240 m in length, were captured and divested of their prey. Collections of prey were subsequently submitted to either Roy Snelling of the Los Angeles County Natural History Museum or John Ascher of the

Fig. 1. A dry wash used as a nesting site by *Aphilanthops hispidus* in the Usery Mountains near Mesa, AZ.

American Museum of Natural History for identification.

To study male behavior, I stood next to plants on the wash border where I could see male wasps flying past. I attempted to capture these individuals in an insect net, and if successful, I marked the captured wasps on the dorsum of the thorax with a DecoColor paint pen before releasing them. All the individuals taken at one spot on the same day initially received the same distinctive color mark (e.g., a red horizontal bar or two white dots). When a marked male was recaptured on the same or subsequent day, it received another color mark that identified it as a particular individual. The mark-recapture data help determine that the males visited a given location over a period of one or more days, a pattern characteristic of patrolling males participating in a scramble competition mating system. In addition, records were made of the reaction of flying males to perched females and to dead pinned specimens that they encountered in the course of their travels.

RESULTS

The mating system of Aphilanthops hispidus.—Early in the flight season, large numbers of males were seen flying rapidly and sinuously in and around the outer portions of flowering creosote bush growing along the 240 m section of the wash where females had nested in the previous year (and where they would nest again in the subsequent year). Later in the flight season, when the acacias along the wash began to bloom, patrolling males flew in and around the outer parts of these plants, having largely abandoned their routes around creosote bush by this time. Thus, from 9 to 18 April 2009, large numbers of males traveled past the creosote bush growing by the nesting/emergence area. But when the first acacia began to flower on 18 April (Fig. 2), patrolling males then appeared at this location. As additional plants came into bloom, male wasp activity shifted almost entirely to these locations. By midday 21 April, only two or three males were seen by the creosote bushes where they had been common earlier, whereas dozens of wasps could be found at the several flowering acacias located 330 to 600 m from the lower end of the creosote bush patrolling area. This pattern persisted through 7 May with the wasps continuing to leave plants that had stopped flowering while shifting to those acacias that had more recently come into full flower.

Although on one day, 21 April 2008, large numbers of males were seen and captured in the latter part of the afternoon at the creosote bush site, patrolling males were far more numerous during mid- to late morning during the 2009 flight season (Fig. 3). The many males counted as they flew past an observation point by a shrub during the short (2 min) sample periods during the peak of male activity in 2009 indicates just how abundant patrollers

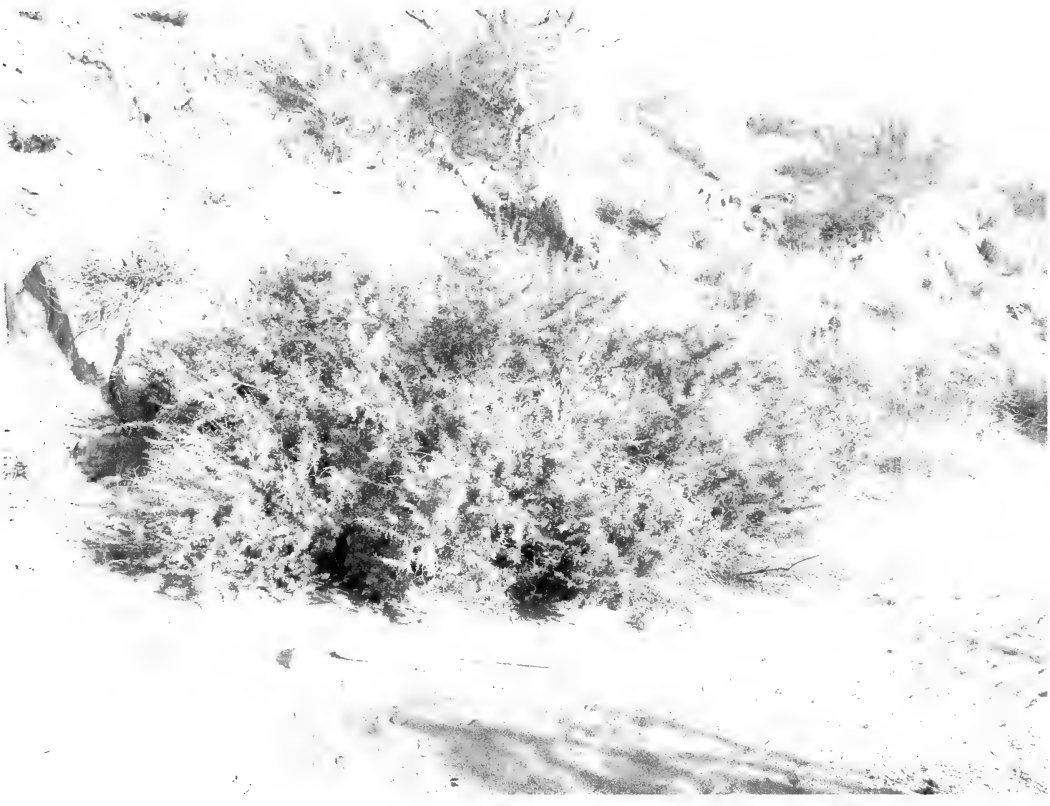


Fig. 2. The first acacia (*Acacia greggii*) to flower and to attract mate-searching males of *Aphilanthops hispidus* in 2009.

were at these times. The fact that only a small proportion of the marked individuals were recaptured on subsequent days also shows that there was a large pool of males visiting particular shrubs. For example, from 22 to 29 April 2009, a total of 82 unmarked males were captured and marked at a set of three acacias growing within 35 m of one another. On 30 April, 18 of 24 males (25%) taken at these plants were unmarked, suggesting a total population of patrollers in the area in the hundreds.

The occurrence of recaptured males demonstrates that at least some males return to locations at or near where they were initially captured. Indeed, all three males that were marked on 30 April 2009 and then recaptured were each taken three

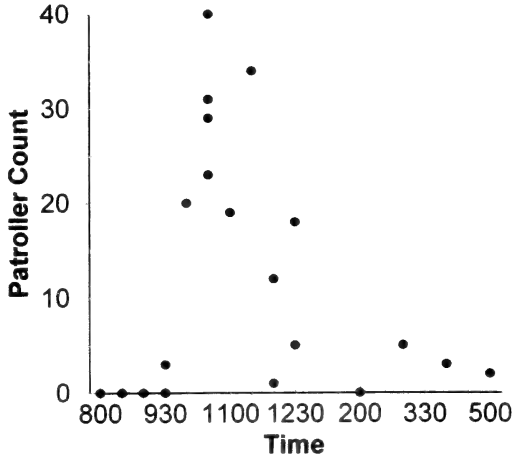


Fig. 3. The number of times a presumptive male of *Aphilanthops hispidus* flew past a fixed point on the exterior of a creosote bush by a nesting/emergence site during a two-min observation period at various times on five days between 9 and 16 April 2009.

times at the same bush in the space of two hours. The three marked males taken on 7 May were recaptured three times each in the space of an hour at a flowering acacia that had not been in full flower on previous visits to the wash but was within 20 m of acacias where patrolling male wasps were seen and taken. Other marked males were also recaptured over a period of two or more days usually at or near the original point of capture (Table 1). The maximum interval between the marking and recapture of any male was six days in 2006, five days in 2007, two days in 2008 and 14 days in 2009 (for two different individuals).

The function of male behavior was revealed when males interrupted their flight forward to zigzag toward females foraging on acacia flowers, where females were commonly seen. A few males made brief contact with the females (N = 7 observations in 2008 and 2009) before resuming their patrol flight. Males also touched pinned, freshly killed females (N = 9 observations), and even attempted copulation, when these females (N = 4) were placed in areas visited by patrolling males. The only naturally occurring mating pair was observed about 1030 M.S.T. on 23 April 2008 as the pair rested in a creosote bush at the edge of the wash in a heavily patrolled corridor (Fig. 4). When the male left his mate, she remained in place for a few minutes and was mounted twice by males that attempted copulation but failed as the female shook herself free on both occasions.

The fact that the vast majority of patrolling males either ignored or merely approached dead nesting females pinned to creosote bush or catclaw acacia suggests that odor cues associated with virgin (?) females are usually necessary to elicit complete copulatory attempts. On the other hand, the fact that a few patrollers pounced very briefly on fellow males and even a honey bee in two instances indicates that visual cues play some role in the acquisition of mates.

Fig. 4. A pair of *Aphilanthops hispidus* perched in a creosote bush along a dry wash that served as a nesting and emergence area for the wasp.

Prey selection by females of Aphilanthops hispidus.—Once females had mated, they appear to have returned to the emergence area to construct their nests given that every year large numbers of burrows were constructed in the same 240 m-long wash

Table 1. Mark-recapture data for male *Aphilanthops hispidus* at the Usery Mountain study site.

Year	Location	Number marked	Number recaptured on-	
			Same day	Subsequent day
2006	Creosote bush	72	0	5 (7%)
2007	Acacia	73	5 (7%)	7 (10%)
2008	Creosote bush	94	0	3 (3%)
2009	Creosote bush	110	7 (6%)	15 (14%)
2009	Acacia	141	13 (9%)	20 (14%)

segment whose borders were patrolled by males each year. Males were never seen inspecting or harassing nesting females at or near their burrows, and thus females, which probably had mated once soon after emergence, were able to dig their nests and to provision them without interference. Prey-laden females flew to their burrow entrances, even when carrying honey bees almost as large as a wasp itself, and hovered there briefly before plunging into the open entrance. If the prey item failed to slip quickly into the tunnel, the wasp entered, turned about, and dragged the prey into the nest.

Females carried prey against their venter, holding the bee or wasp with their midlegs (Fig. 5). They provisioned the nest primarily with honey bees and native bees (Table 2), although occasionally they utilized small wasps. Five families of bees are represented in the prey list. Nesting in 2009 began at a time when the creosote bushes still had some bee-attracting flowers but by late April and early May, when nest provisioning was still occurring, the local creosote bush had largely completed flowering. At this time, females of *A. hispidus* were regularly seen foraging for nectar on catclaw acacias but they were not seen hunting for prey at these plants.

Fig. 5. A female of *Aphilanthops hispidus* waiting in a cresosote bush after having been disturbed as she attempted to enter her nest with prey, a honey bee.

DISCUSSION

Males of *A. hispidus* appeared to be engaged in a scramble competition for mates with individuals patrolling the borders of a large emergence area from which many virgin females emerge each year. Searching males also flew past flowering acacias known to attract nectar-foraging females. The fact that males often fly upwind close to or within the outer portions of selected plants suggests that they are searching for odor and visual cues associated with receptive females perched in the vegetation. The infrequency with which matings were observed in this study and the lack of interest males showed in provisioning females suggests that females of *A. hispidus* mate just once, as appears to be the typical pattern in crabronid wasps and many other Hymenoptera (Hughes et al. 2008; Paxton 2005; Strassmann 2001). If true for *A. hispidus* as well, then males that reach virgin females first presumably gain a large fitness advantage over their rivals. However, if virgin females only emerge in the first few weeks of the flight season, one would not predict that males would continue to be found patrolling for mates a month after they were first seen, as was the case in 2009. Perhaps some females emerge late in the flight season or perhaps some mate more than once.

Scramble competition for mates has evolved many times in insects (Seidemann 1999; Thornhill and Alcock 1983) and other animals (e.g., Kappeler et al. 2002; Schwagmeyer 1988). This mating system appears to be associated with evenly or unpredictably distributed receptive females coupled with the presence of many competing males. These factors apply to *A. hispidus* at the Usery Mountain site given the large

Table 2. The prey selected by provisioning females of *Aphilanthops hispidus*.

2007	2008	2009
Colletidae		
Colletes circidii Timberlake (4)	*Colletes* sp. (2)	*Colletes* sp.
Megachilidae		
Trachusa larreae (Cockerell)	*T. larreae* (2)	
Megachile odontostoma Cockerell	*Megachile* sp. (3)	*Megachile* sp.
Megachile newberryae Cockerell		
Megachile gentilis Cockerell		
		Anthidium sp.
		Osmia subfasciata Cresson (2)
Andrenidae		
Andrena prunorum Cockerell	*Andrena* sp.	
	Andrena candida Smith	*A. candida* (2)
	Andrena fracta Cassad & Cockerell	*A. fracta* (9)
	Ancylandrena larreae (Timberlake)	*A. larreae*(2)
Halictidae		
Nomia melanderi Cockerell (2)		
	Nomia howardi Cockerell	
	Nomia tetrazonta Cockerell	*N. tetrazonta* (2)
Lasioglossum sisymbrii (Cockerell)	*L. sisymbrii*	
Apidae		
Diadasia rinconis Cockerell		
	Anthophora sp. (3)	
	A. californica Cresson	
	Nomada sp.	
	Ericrocis lata (Cresson)	*E. lata*
		Melissodes paroselae Cockerell
		Epeolus sp.
		Habropoda pallida (Timberlake)
Apis mellifera Linnaeus	*A. mellifera* (26)	*A. mellifera* (16)

number of nests scattered more or less evenly over a long segment of wash from which many virgin females and males emerge during the flight season. Any male that attempted to defend a territory would be in possession of only a small fraction of a plant where the probability that a virgin female would arrive was no greater than elsewhere. Moreover, the territorial individual would constantly have to respond to passing males, whose entry into his defended space would be costly to prevent.

The scramble competition mating system of *A. hispidus* differs markedly from the mating system of its congener, *A. subfrigidus* (O'Neill 1990). Males of that species defend small display territories close to those of several other males. The males' territories are clustered in areas where *Formica* ant alates are swarming. Each individual at the lek appears to mark his site with an attractant pheromone while chasing and even grappling with any fellow males that enter his territory. Receptive females may visit these sites to select a partner from among those present, although mating has not been observed in this species.

Males of *A. subfrigidus* possess paired hairbrushes along the outer portion of the lower margin of the clypeus that they appear to use to mark vegetation in their territories with pheromones from glands in the head in the manner of their relatives in the genus *Philanthus* (Evans and O'Neill 1988). The fact that males of *A. hispidus* also possess clypeal brushes of about the same size as those of *A. subfrigidus* (Kevin O'Neill, personal communication) raises the possibility that some males under some

circumstances may engage in scent marking in an alternative mating system yet to be observed in this species.

The ecology of *A. subfrigidus* is similar but not identical to that of *A. hispidus* (O'Neill 1990). Females of *A. subfrigidus* do form nesting aggregations but these are small with many fewer individuals than present at the Usery Mountain *A. hispidus* site. The smaller number of nesting females in populations of *A. subfrigidus* must translate into fewer adult males, which in turn could make the costs of male territoriality less for this species, and thus more likely to evolve. In addition, by placing their display territories within ant swarm sites, males of *A. subfrigidus* may be taking advantage of the attraction of the prey resource for females of their species. Much still remains to be learned, however, about why lek territoriality evolves in some species while related ones exhibit scramble competition polygyny (Thornhill and Alcock 1983).

Prey selection by Aphilanthops hispidus.—Females of *A. hispidus* are generalist predators that take a wide variety of solitary bees, as well as the introduced honey bee, which was by far the most commonly captured prey species at this study site over the years. Interestingly, Evans found native bees belonging to four families in a cache of seven individuals within an excavated nest (Evans 1977), suggesting that individual wasps do not specialize on one or a few of the prey species available to them. Females of *A. hispidus* also take the occasional wasp but were not observed with ants, the sole prey of the well-studied *A. frigidus* (Evans 1962, 1970) and *A. subfrigidus* (Bohart 1966; O'Neill 1990). It seems likely that females of *A. hispidus* exploit any bees of suitable size, especially those that visit creosote bush for nectar or pollen. Thirteen of the species on the prey list from the Userys (Table 2) also appear on the list of native bees collected at one or more of 47 *Larrea* sites studied by Minckley et al. (1999). In addition, seven wasps were taken from provisioning females in three years (2007–2009), including a vespid, *Parancistrocerus toltecus* (de Saussure), another eumenine and five other wasps that have unfortunately been misplaced.

With respect to prey selection, *A. hispidus* is more similar to the generalist bee and wasp predators in the genus *Philanthus* than it is to others in its own genus, which apparently take only ants (alate queens of *Formica* in the case of *A. frigidus* and *A. subfrigidus*) as is also true for wasps in the closely related philanthine genus *Clypeadon*, although these species hunt worker ants rather than reproductives (see review in Evans and O'Neill (1988)).

ACKNOWLEDGMENTS

I am grateful to Kevin O'Neill for his instructive review of the manuscript and his willingness to examine specimens of *A. hispidus* to see if males possess clypeal hairbrushes. Bill Rubink also helped improve the manuscript. Thanks to John Ascher for identifying two samples of prey taken by females of *A. hispidus*. For the first batch of prey, I called on Roy Snelling to help, which he did with his characteristic professionalism and generosity. I dedicate this paper to the memory of Roy Snelling.

LITERATURE CITED

Bohart, R. M. 1966. A review of *Aphilanthops* and related genera (Hymenoptera: Sphecidae). *Proceedings of the Entomological Society of Washington* 68: 158–167.

Evans, H. E. 1962. A review of the nesting behaviour of digger wasps of the genus *Aphilanthops*, with special attention to the mechanism of prey carriage. *Behaviour* 19: 239–260.

———. 1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. *Bulletin of the Museum of Comparative Zoology* 140: 451–511.

———. 1977. *Aphilanthops hispidus* as a predator of bees (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist* 53: 123.

——— and K. M. O'Neill. 1988. *The Natural History and Behavior of North American Beewolves*. Cornell University Press, Ithaca, N.Y. 278 pp.

Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral monogamy shows kin selection is key to evolution of sociality. *Science* 320: 1213–1216.

Kappeler, P. M., B. Wimmer, D. Zinner, and D. Tautz. 2002. The hidden matrilineal structure of a solitary lemur: implications for primate social

evolution. *Proceedings of the Royal Society of London B* 1502: 1755–1763.

Minckley, R. L., J. H. Cane, L. J. Kervin, and T. H. Roulston. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society* 67: 119–147.

O'Neill, K. M. 1990. Female nesting behavior and male territoriality in *Aphilanthops subfrigidus* Dunning (Hymenoptera, Sphecidae). *Pan-Pacific Entomologist* 66: 19–23.

Paxton, R. J. 2005. Male mating behaviour and mating systems of bees: an overview. *Apidologie* 36: 145–156.

Schwagmeyer, P. L. 1988. Scramble-competition polygyny in an asocial mammal: Male mobility and mating success. *American Naturalist* 131: 885–892.

Seidemann, K. 1999. The race for females: The mating system of the red mason bee, *Osmia rufa* (L.) (Hymenoptera : Megachilidae). *Journal of Insect Behavior* 12: 13–25.

Strassmann, J. E. 2001. The rarity of multiple mating by females in the social Hymenoptera. *Insectes Sociaux* 48: 1–13.

Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA. 547 pp.

J. HYM. RES.
Vol. 18(2), 2009, pp. 175–177

A Dense Daytime Aggregation of Solitary Bees (Hymenoptera: Apidae: Centridini) in the Lesser Antilles

CHRISTOPHER K. STARR AND DANNY VÉLEZ

(CKS, DV) Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad & Tobago
(DV) Current Address: Departamento de Biología, Universidad Nacional de Colombia, AA 14490, Santafé de Bogotá, Colombia

Abstract.—A dense daytime aggregation of thousands of bees was present on at least six successive days on a large *Caesalpinia bonduc* (Caesalpiniaceae) shrub on the island of Anguilla, Lesser Antilles. A sample consisted of both sexes of *Centris (Centris) decolorata*, *C., (C.) smithii* and *C. (Hemisiella) lanipes*, with the bulk of individuals being males of *C. decolorata*. The unusual features of the aggregation were its persistence during daylight hours, the presence of multiple species, and the presence of females. The three species are new records for Anguilla.

Key words.—Anguilla, Apoidea, bees, *Centris*, Lesser Antilles

Many solitary wasps and bees are known to form more or less dense clusters of individual during daily inactive periods (Evans and Linsley 1960; Linsley 1962; O'Neill 2001:293–296; Azevedo and Faria 2007; Alves-dos-Santos et al. 2009). Commonly known as "sleeping aggregations", this phenomenon is so widespread that some authors (e.g. Gess 1966:63) make a point of noting species in which it is not observed. As a rule, aggregations each comprise a single species and sex, usually males, with some known exceptions (e.g. Evans 1966:429–431). Daytime aggregations during clement weather are almost unknown; in the one reported instance of which we are aware, Starr and Hernández (1995) reported a sunny-afternoon aggregation of male *Pepsis sericans* Lep. (Pompilidae) in Cuba. Evans and Linsley (1962) reviewed three possible explanations for wasp and bee aggregations given by Rayment (1935), Grassé (1942) and themselves: a) as a preliminary stage in the evolution of social habits, b) increased temperature through dense clustering, and c) improved vigilance against predators. Alcock (1998) suggested that in *Idiomelissodes duplocincta* (Cockerell, 1905) (Apidae: Eucerini) aggregation could provide d) anti-predator benefits through a dilution effect.

Members of the genus *Centris* Fabricius, 1804 are solitary bees, well distributed in the northern Neotropics, including the West Indies (Snelling 1984; Moure *et al.* 2007; Genaro and Franz 2008). Nighttime aggregation of males are known for *C. adani* Cockerell, 1949, *C. fuscata* Lepeletier, 1841 (Frankie et al. 1980; Azevedo and Faria 2007) and *C. decolata* Lepeletier, 1841 (Alves-dos-Santos et al. 2009). Relationships between several species of *Centris* and plants of the genus *Caesalpinia* (Caesalpiniaceae) have been reported. *Centris* spp. have been observed collecting nectar on *Caesalpinia* spp. (Vinson et al.1996; Aguiar et al. 2003), and studies of nest resources have shown the presence of pollen from *Caesalpinia* spp. (Quiroz-García et al. 2001).

We describe here an especially large aggregation of *Centris* and report for the first time the presence of three species in Anguilla, Lesser Antilles.

All field observations (by CKS) are from 22–27 August 2006 (mid-rainy season) at

Windward Point on the island of Anguilla. Windward Point is a low, open area with a limestone substrate and sparse, cactus-dominated vegetation. Specimens collected in Anguilla 2006 and identified as *C. (C.) smithii* Cresson, 1879, *C. (C.) decolorata* Lepeletier, 1841 and *C. (H.) lanipes* (Fabricius, 1775) will serve as vouchers. These are at present deposited in the Land Arthropod Collection of the University of the West Indies (Trinidad & Tobago) and in the Bee Collection of the Pontificia Universidad Católica de Valparaíso (Chile).

During mid- to late-morning on each of six consecutive days, an extremely large, dense aggregation of *Centris* bees was observed in the crown of a dense blooming shrub of *Caesalpinia bonduc* (L.) Robx. (Caesalpiniaceae), a common plant in dry environments near the beach. The shrub was about 1.5–1.8 m tall and covered an area of roughly 5 m^2. The bees were mostly a very few centimeters inside the outer layer of the shrub. While undisturbed, they moved very little, with almost no flying into or out of the aggregation. Shaking the shrub produced a furious swarming out and around the shrub for a few minutes, followed by a return to the aggregation.

Because the bees were mostly hidden in the shrub, we can only estimate the number of individuals at several thousands. A sample from the aggregation showed that most individuals (93%) were males of *C. decolorata*, with minor fractions of female *C. decolorata*, and *C. smithii* and *C. lanipes* of both sexes (Table 1).

Three features make this an unusual aggregation: a) it was present in the daytime, b) it comprised multiple species, and c) females were present among the males. Of the four suggested explanations for aculeate aggregations noted above, (a) can be rejected out of hand, and (b) makes little sense in the climate of Anguilla. The late morning is a relatively inactive time of day for many bees, so that it might have been a true resting aggregation. Under these circumstances, it is plausible that aggregation served a defensive function through (c) improved vigilance and/or (d) dilution. The swarm-flying response of the bees to disturbance is consistent with this hypothesis. The present observations were made incidental to quite a different study restricted to morning hours (about 09:00–12:00), so we do not know whether the same site served as a roost at other times of the day or night.

Table 1. Composition of a sample from a dense aggregation of solitary bees on a *Caesalpinia bonduc* bush on Anguilla, Lesser Antilles.

	Males	Females	Total
Centris decolorata	241	5	246
Centris smithii	4	7	11
Centris lanipes	1	1	2
Total	246	13	259

We have found no report of any *Centris* species from the island of Anguilla. All three species are evidently new records.

ACKNOWLEDGMENTS

We thank Keith David and JoAnne Sewlal for assistance in the field, Winston Johnson for identifying *C. bonduc*, Julio Genaro and Felipe Vivallo for confirming identifications of the bees, Adam Roddy for sending literature, and Victor H. González and the journal's reviewers for criticism of an earlier version of this note.

LITERATURE CITED

Aguiar, C. M. L., F. C. V. Zanella, C. F. Martins, and C. A. L. de Carvalho. 2003. Plantas visitadas por *Centris* spp. (Hymenoptera: Apidae) na Caatinga para obtenção de recursos florais. *Neotropical Entomology* 32: 247–259.

Alcock, J. 1998. Sleeping aggregations of the bee *Idiomelissodes duplocincta* (Cockerell) (Hymenoptera: Anthophorini) and their possible function. *Journal of the Kansas Entomological Society* 71: 74–84.

Alves-dos-Santos, I., M. C. Gaglianone, S. R. C. Naxara, and M. S. Engel. 2009. Male sleeping aggregations of solitary oil-collecting bees in Brazil (Centridini, Tapinotaspidini, and Tetrapediini; Hymenoptera: Apidae). *Genetics and Molecular Research* 8: 515–524.

Azevedo, A. A. and L. R. R. Faria. 2007. Nests of *Phacellodomus rufifrons* (Wied, 1821) (Aves: Fur-

nariidae) as sleeping shelter for a solitary bee species (Apidae: Centridini) in southeastern Brazil. *Lundiana* 8: 53–55.

Evans, H. E. 1966. *The Comparative Ethology and Evolution of the Sand Wasps*. Cambridge: Harvard University Press, 526 pp.

——— and E. G. Linsley. 1960. Notes on the sleeping aggregation of solitary bees and wasps. *Bulletin of the Southern California Academy of Sciences* 59: 30–37.

Frankie, G. W., S. B. Vinson, and R. E. Coville. 1980. Territorial behavior of *Centris adani* and its reproductive function in the Costa Rican dry forest (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* 53: 837–857.

Genaro, J. A. and N. M. Franz. 2008. The bees of Greater Puerto Rico (Hymenoptera: Apoidea: Anthophila). *Insecta Mundi* 40: 1–24.

Gess, S. K. 1996. *The Pollen Wasps*. Cambridge: Harvard University Press, 340 pp.

Grassé, P.-P. 1942. Les rassemblements de sommeil des Hyménoptères et leur interprétation. *Bulletin de la Société Entomologique de France* 47: 142–148.

Linsley, E. G. 1962. Sleeping aggregations of solitary Hymenoptera – II. *Annals of the Entomological Society of America* 55: 148–164.

Moure, J. S., G. A. R. Melo, and F. Vivallo. 2008. Centridini Cockerell & Cockerell, 1901. *In* Moure, J. S., D. Urban, and G. A. R. Melo, eds. *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*. http://www.moure.cria.org.br/catalogue. Accessed 10 May 2009.

O'Neill, K. M. 2001. *Solitary Wasps*. Ithaca: Cornell University Press, 406 pp.

Quiroz-García, D. L., E. Martínez-Hernández, R. Palacios-Chávez, and N. E. Galindo-Miranda. 2001. Nest provisions and pollen foraging in three species of solitary bees (Hymenoptera: Apidae) from Jalisco, Mexico. *Journal of the Kansas Entomological Society* 74: 61–69.

Rayment, T. 1935. *A Cluster of Bees*. Endeavour, Sydney752 pp.

Snelling, R. R. 1984. Studies on the taxonomy and distribution of American centridine bees (Hymenoptera: Anthophoridae). *Contributions in Science* (Los Angeles) 347: 1–69.

Starr, C. K. and L. R. Hernández. 1995. A daytime resting aggregation of male *Pepsis sericans* (Pompilidae). *Sphecos* 29: 12–13.

Vinson, S. B., G. W. Frankie, and H. J. Williams. 1996. Chemical ecology of bees of the genus *Centris* (Hymenoptera, Apidae). *Florida Entomologist* 79: 109–129.

J. HYM. RES.
Vol. 18(2), 2009, pp. 178–182

A New Subgenus and Species of Neotropical *Hylaeus* from Costa Rica (Hymenoptera: Colletidae)

TERRY GRISWOLD

USDA-ARS Bee Biology & Systematics Laboratory,
Utah State University, Logan, Utah 84322-5310, USA

Abstract.—A new Neotropical subgenus of *Hylaeus*, ***Snellingella*, subgenus nov.**, is described, with ***Hylaeus amplus*, sp. nov.**, from Costa Rica as the type species. Characteristics to separate the new species from other Costa Rican *Hylaeus* are provided.

Hylaeus Fabricius is a diverse genus (47 subgenera, over 700 species) with one of the broadest distributions of any genus of bees. *Hylaeus* is found on all continents except Antarctica and on remote islands, and is diverse in both temperate and tropical regions (Michener 1979). In the Neotropical Region, 111 species are recognized (Moure et al. 2007), with most of the South American species unplaced to subgenus. Subgenera recorded from the Neotropics include *Cephylaeus* Moure (southern Brazil), *Gongyloprosopis* Snelling (tropical South America), *Hylaeopsis* Michener (Neotropical Region), *Hylaeana* Michener (Neotropical Region), *Orohylaeus* Michener (high Andes), *Prosopis* Fabricius (Holarctic, northern margin of the Neotropical Region), and *Spatulariella* Popov (adventive in Chile and Argentina).

Roy Snelling contributed much to our knowledge of this challenging group. He revised the *Hylaeus* of the Nearctic region (Snelling 1966a, 1966b, 1966c, 1968, 1970), southern India and Sri Lanka (Snelling 1980) and the Bonin Islands (Snelling 1970), and published works on *Hylaeus* of the Afrotropics (Snelling 1985) and Neotropical region (Snelling 1982). It is therefore fitting to describe a distinctive Neotropical *Hylaeus* from Costa Rica in his honor.

METHODS

Distinguishing between subgeneric and specific characters in an, at present, monotypic subgenus is fraught with risk. Here, characters that are used to recognize existing subgenera are included in the subgeneric description; characters that vary within other Neotropical subgenera are included in the species description. Morphological terminology follows Michener (2007) and for propodeal structures Snelling (1985). The abbreviations F1, F2, etc., denote the first, second, etc. flagellar segments of the antenna; T1, T2, etc. the first, second, etc. metasomal terga; S1, S2, etc., the first, second, etc. metasomal sterna.

Snellingella new subgenus

Type species: *Hylaeus amplus*, sp. nov.

Diagnosis.—This subgenus is distinguished from all other Western Hemisphere subgenera (and representatives of the 25 of 36 subgenera not native in the Americas available for study) by the V-shaped basal depression of T1 punctate rather than impunctate. The combination of head wider than long, linear malar space, non-carinate pronotal lobe and omaulus, complete apical hair band on

T1, and T2 with gradulus, also serve to distinguish it.

Description.—Head short, broad (Figs 1,2). Interantennal platform weakly developed, not carinate laterally. Malar space linear. Pronotal collar narrow especially medially, lateral angle in dorsal view obliquely angled, not truncate. Pronotal lobe broadly rounded, without dorsal carina, lacking distinct anterior face. Scutum in profile convex anteriorly, well above pronotal collar. Omaulus not carinate. Propodeum except basal area and propodeal pit obscured by pubescence; propodeal triangle with basal portion strongly sloping, lateral margin carinate, without carina separating it from posterior area; no carina enclosing spiracle. Forecoxa not carinate, without lateral process or spine. T1 V-shaped basal depression punctate, with lateral margin not sharply angled; apical margin of segment with strong apical hair band, other terga with bands indistinct or absent. T2 with distinct, shallow gradulus, carinate on anterior margin.

Male.—Mandible bidentate, inner tooth not as long as outer, apices acute. Facial fovea small, linear, indistinct among coarse punctures. Preoccipital carina present dorsally and laterally. T1 in lateral view without distinct angle between anterior and dorsal faces. T2 gradulus narrow. S8 distal process narrowly keeled, straight, not bent down. Genitalia with gonstylus broad, not rod-like apically.

Female.—Facial fovea short, not quite reaching level of anterior margin of lateral ocellus, nearer to eye than to ocellus. Vertex bulging in area of ocelli. Preoccipital carina present dorsally, not laterally. T1 in lateral view evenly curved without distinct anterior and dorsal faces. T2 gradulus broad. Sterna punctate, surface not satiny.

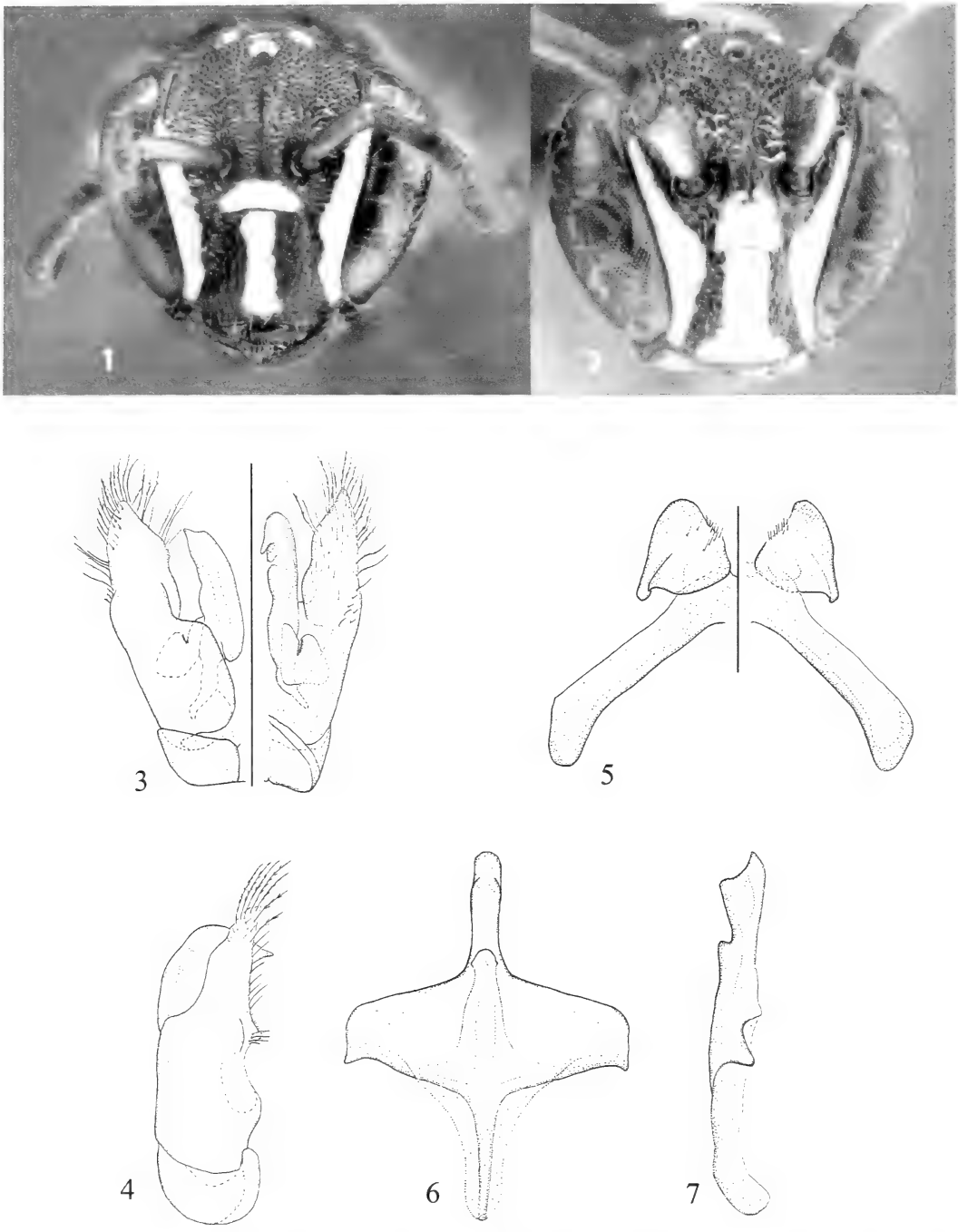
Discussion.—In the keys to subgenera of the Western Hemisphere (Snelling 2007), males run to couplet 7 where they agree with *Hylaeus* s. str. in the parallel sided interantennal elevation that extends dorsally beyond the antennal sockets, but they lack pectinate apical lobes on S7. Females run to couplet 6 where they fail to agree with either option; the gena is as wide as the eye and the mesepisternal punctures are distinct, but lateral carinae are present on the propodeum and the terga are conspicuously, densely punctate.

Etymology.—It is a great pleasure to recognize a friend and colleague who has contributed much to our knowledge of bees in general and *Hylaeus* in particular. Roy took the time to encourage a young high school teacher attempting to do systematic work on the side, even turning over a mostly completed manuscript. For that I will always be grateful.

Hylaeus (*Snellingella*) *amplus* new species
(Figs 1–7)

Diagnosis.—The subgeneric diagnosis will serve to differentiate *H. amplus* from other Western Hemisphere species. In addition, male S7 (Fig. 5) and S8 (Figs 6, 7) are unique. Among the 26 species known from Costa Rica (Griswold et al 1995, updated), some undescribed, *H. amplus* can be distinguished by the combination of scutellum not maculate, propodeum without transverse carina, mesepisternum sparsely punctate and shiny, T1 with complete apical hair band, and T2 with distinct gradulus.

Male.—Body length 8 mm, forewing length 5.5 mm. Integument black except: yellow on mandible, labrum medially, clypeus except along lateral margin, supraclypeal area, paraocular area, scape ventrally, pronotal collar, posterior spot on pronotal lobe, spot on tegula, foretibia anteriorly, midtibia apically on anterior surface, hindtibia basal stripe anteriorly, all basitarsi; various shades of reddish brown on antenna, legs, lateral and apical margins of terga, sterna apically. Wings stained, strongly so anteriorly on forewing, veins dark brown. Pubescence white ex-



Figs 1–7. *Hylaeus* (*Snellingella*) *amplus* new species. 1, Head of female. 2, Head of male. 3, Dorsal, ventral views of male genitalia. 4, Lateral view of male genitalia. 5, Dorsal, ventral views of male S7. 6, Ventral view of male S8. 7, Lateral view of male S8.

cept dark on T7, S6; longest hairs shorter than scape; erect on head, moderately dense on hypostomal area; very short, sparse on scutum; dense on metanotum laterally; obscuring integument on mesepisternum ventrally and most of propodeum; T1 with narrow apical band of short, dense, plumose hairs obscuring surface; T2–5 with short, sparse pubescence not forming distinct apical bands. Body dull except shiny on mesepisternum, lateral face of propodeum, T1, sterna; surface, where punctures not contiguous, lineolate; punctures of clypeus, paraocular area, supraclypeal area indistinct, separated by one to two puncture widths; frons, vertex irregularly contiguously punctate; scutum, scutellum densely but not contiguously punctate; mesepisternum with punctures small, two to three puncture widths apart; metepisternum transversely striate throughout; propodeum laterally finely, densely, but not contiguously, punctate; T1 punctures dense, coarse on dorsal surface, nearly contiguous medially; T2 more densely, finely punctate; T3–5 still more finely punctate; sterna with fine, sparse punctation.

Head broader than long (1.1 ×, Fig. 2). Ocelloccipital distance < interocellar distance < ocellocular distance. Maximum genal width less than maximum eye width in lateral view (0.9 ×). Scape moderately expanded, length approximately 1.5 times maximum width; F1 broader than long (1.4 ×); F2 length 1.1 times width; F3 length 1.3 times width, F4–10 similarly shaped. Propodeum with well developed lateral and oblique carinae, dorsal surface shorter than scutellum, basal zone coarsely rugulose, delimited laterally by irregular carina, propodeal pit slender, elongate, narrowed dorsally, propodeal spiracle not delimited by carina. T1 narrowly depressed apically. T2 more broadly, strongly depressed apically behind lateral preapical swelling. T3 with broad, slightly depressed apical area. S7 as in Fig. 5. S8 as in Figs 6, 7. Genitalia as in Figs 3, 4.

Female.—Length 7.5–8.5 mm; forewing length 6.5–7 mm. As in male except for usual sexual differences and as follows: yellow markings restricted to wide longitudinal stripe on clypeus, supraclypeal area, paraocular area (Fig. 1), pronotal collar. Pubescence sparser on hypostomal area, denser on propodeum, T2–4 margins, sterna. Punctation finer on frons, vertex, scutum, scutellum, terga; sparser on scutum, scutellum; denser on sterna.

Head broader than long (1.2 ×). Maximum genal width equal to maximum eye width in lateral view (1.0 ×). Scape not expanded; F1 slightly wider than long (1.1 ×); F2 wider than long (1.2 ×); F3–9 as long, or slightly longer, as wide (1.0–1.1 ×). Propodeum basal zone slightly less coarsely rugulose. T2 not strongly depressed apically; T3 scarcely depressed apically. T2–3 with circular lateral fovea covered with appressed setae.

Type Material.—Holotype male: **Costa Rica**, San Jose, Escazu, 24–30 Jan 1988, F. D. Parker (#30778). Paratypes: **Costa Rica**: 1 male, San Jose, Escazu, 5 Feb 1989, F. D. Parker; 1 female, San Jose, San Isidro General, Feb 1993, F. D. Parker; 1 female, Guanacaste, Finca Montezuma, 3 km SE Rio Naranjo, 25–31 Mar 1992, F. D. Parker; 1 female, same except 12–20 Mar 1993. Holotype and paratypes in the U. S. National Pollinating Insects Collection, Logan, Utah.

Distribution.—Apparently endemic to mid elevations of Costa Rica.

Discussion.—*Hylaeus amplus* is rarely collected. Of 565 specimens of Costa Rican *Hylaeus* studied, only five specimens belong to this species. All were collected in the months of January through March even though at two of the localities collections were made throughout the entire year.

Etymology.—This bee is significantly larger than any other Costa Rican *Hylaeus*, thus the Latin *amplus*, large.

ACKNOWLEDGMENTS

Frank Parker's tireless efforts to survey the bees of Costa Rica made this work possible. Illustrations were

rendered by Victor Gonzalez; pictures of heads provided by Harold Ikerd. I am grateful to Charles Michener and Kevin Williams for reviewing the manuscript.

LITERATURE CITED

Michener, C. D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* 66: 277–347.

———. 2000. A high Andean subgenus and species of *Hylaeus* (Hymenoptera, Colletidae). *Journal of the Kansas Entomological Society* 73: 1–5.

———. 2007. *The Bees of the World*. 2nd Edition. Johns Hopkins University Press, Baltimore, Maryland. xvi+ 953 pp.

Moure, J. S., D. Urban, and G. A. R. Melo, eds. 2007 *Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical Region*. Sociedade Brasileira de Entomologia, Curitiba. 1058 pp.

Snelling, R. R. 1966a. Studies on North American bees of the genus *Hylaeus*, 1. Distribution of the western species of the subgenus *Prosopis* with description of new forms. *Contributions in Science, Los Angeles County Museum of Natural History* 98: 1–18.

———. 1966b. Studies on North American bees of the genus *Hylaeus*, 2. Description of a new subgenus and species. *Proceedings of the Biological Society of Washington* 79: 139–144.

———. 1966c. Studies on North American bees of the genus *Hylaeus*. 3. The nearctic subgenera. *Bulletin of the Southern California Academy of Sciences* 65: 164–175.

———. 1968. Studies on North American bees of the genus *Hylaeus*, 4. The subgenera. *Cephalylaeus, Metziella and Hylaeana. Contributions in Science, Los Angeles County Museum of Natural History* 144: 1–6.

———. 1970. Studies on North American bees of the genus *Hylaeus*, 5. The subgenera *Hylaeus* s. str. and *Paraprosopis*. *Contributions in Science, Los Angeles County Museum of Natural History* 180: 1–59.

———. 1970. The *Hylaeus* of the Bonin Islands, western Pacific Ocean (Hymenoptera Colletidae). *Bulletin of the Southern California Academy of Sciences* 69: 1–19.

———. 1980. New bees of the genus *Hylaeus* from Sri Lanka and India. *Contributions in Science, Natural History Museum of Los Angeles County* 328: 1–18.

———. 1982. The taxonomy of some neotropical *Hylaeus* and descriptions of new taxa. *Bulletin of the Southern California Academy of Sciences* 81: 1–25.

———. 1985. The systematics of the hylaeine bees (Hymenoptera: Colletidae) of the Ethiopian zoological region: The genera and subgenera with revisions of the smaller groups. *Contributions in Science, Natural History Museum of Los Angeles County* 361: 1–33.

———. 2007. Key to the subgenera of *Hylaeus* of the Western Hemisphere. *In* C. D. Michener. *Bees of the World*. Baltimore: John Hopkins University Press.

J. HYM. RES.
Vol. 18(2), 2009, pp. 183–191

A Revision of *Dianthidium* Subgenus *Mecanthidium* Michener (Hymenoptera: Megachilidae)

DAVID A. TANNER*, TERRY GRISWOLD AND JAMES P. PITTS

(DAT, JPP) Department of Biology, Utah State University, Logan, UT 84322, USA
(TG) USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah, USA

Abstract.—The resin bees of *Dianthidium* subgenus *Mecanthidium* Michener are revised. Three species, all endemic to Mexico, are recognized: ***D. snellingi* Tanner and Griswold, sp. nov.**, from Jalisco, ***D. zapotecum* Tanner and Griswold, sp. nov.**, from Oaxaca and Chiapas; and the highly variable *D. macrurum* Cockerell from central Mexico. *Dianthidium sonorum* Michener is regarded as a new synonym of *D. macrurum*. A key to the species is provided.

Among the more interesting bees in the genus *Dianthidium* Cockerell (Hymenoptera: Megachilidae) are large reddish-brown bees of the subgenus *Mecanthidium* Michener. These uncommon bees, endemic to Mexico, have been recorded from the coastal states of Nayarit, Jalisco, and Colima, east into Morelos, and in the southern state of Oaxaca. Little is known about their floral host preferences or natural history, aside from nesting habits (Parker 1977). *Mecanthidium* was originally placed in *Paranthidium* Cockerell due to the long, oblique apical margin on the female mandible. Later, based on shared synapomorphies (see below), Griswold and Michener (1988) transferred *Mecanthidium* to *Dianthidium*. The placement in *Dianthidium* is also supported by similarities in nesting habits with other subgenera of the genus (Parker 1977). Nests are primarily made of tree resins (Parker 1977); in *D. macrurum* Cockerell, nests are built in crevices (e.g., crevices between rocks) using small pebbles held together with resin. There can be multiple stories of cells within a single nest, but the orientation and arrangement of cells is variable.

Roy Snelling had recognized a new species in this group and sent it to Terry Griswold. Here, in revising this distinctive and little known group of resin bees, we wish to recognize his significant contribution to the taxonomy and systematics of bees.

* Corresponding Author

MATERIALS AND METHODS

Pinned specimens of all included species were examined with a Motic K-series stereomicroscope. Genitalia were dissected and illustrated using a camera lucida. Morphological terminology follows Michener (2007) including use of the term "preomaular area" for the anterior face of the mesepisternum, which in *Mecanthidium* is dorsally set off from the lateral face by the omaular carina. We use the abbreviation T1, T2, ... T7 to denote metasomal terga 1, 2, ... 7, and S1, S2, ... S6 to denote metasomal sterna 1, 2, ... 6. Plumose setae refer to setae with branches longer than the width of the central shaft.

Institutions.—

BBSL	U.S. National Pollinating Insect Collection, USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah, USA.
CASC	California Academy of Sciences, San Francisco, California, USA.
CISC	Essig Museum of Entomology, Department of Entomological

Sciences, University of California, Berkeley, California, USA.

LACM Insect Collection, Los Angeles County Museum of Natural History, Los Angeles, California, USA.

NMNH National Museum of Natural History, Washington, D.C., USA.

Dianthidium (*Mecanthidium*) Michener

Paranthidium subg. *Mecanthidium* Michener, 1942. N. Y. Entomol. Soc., Jour. 50: 278. Type-species: *Paranthidium* (*Mecanthidium*) *sonorum* Michener.

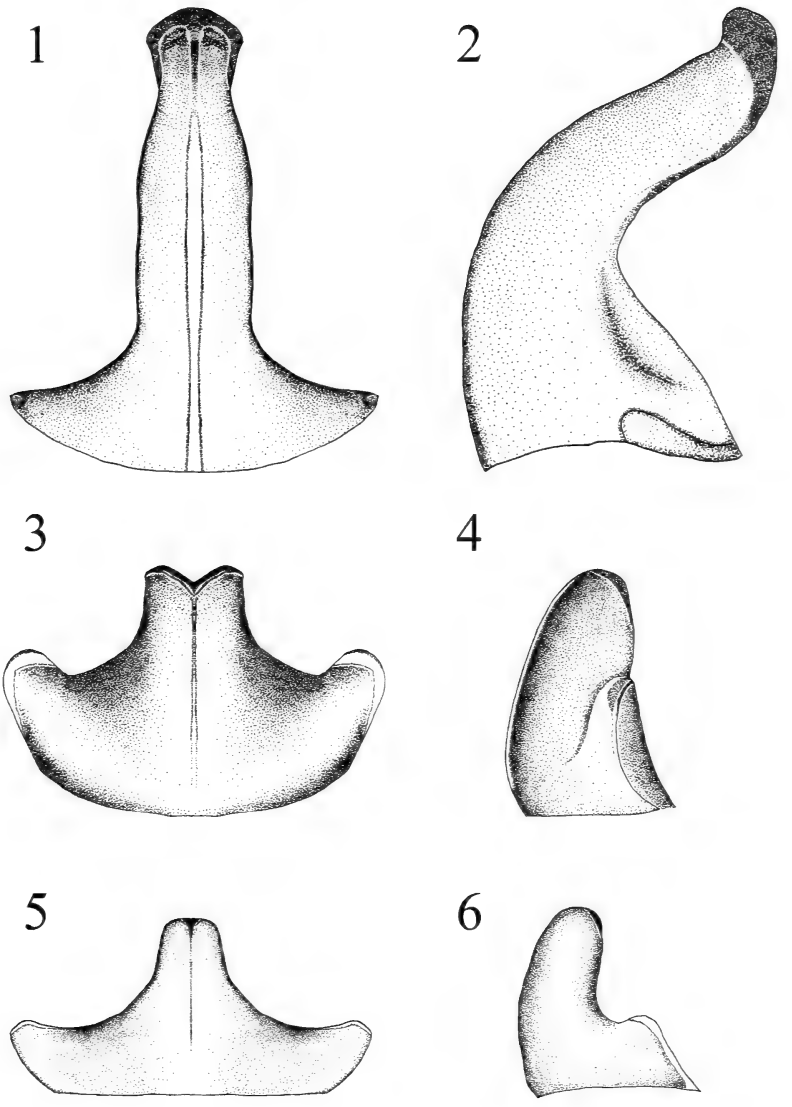
Dianthidium subg. *Mecanthidium* Griswold and Michener, 1988. Jour. Kansas Entomol. Soc. 61: 33.

Diagnosis.—*Mecanthidium* is readily distinguished from all other Mexican Anthidiini except *Aztecanthidium* Michener and Ordway by its reddish brown color (without or with indistinct yellow bands on the terga). From *Aztecanthidium* it differs by the absence of a preoccipital carina, pronotal lobe lamellate and widest behind middle, and the presence of a postspiracular fovea on the propodeum. Males can be distinguished from *Paranthidium*, *Aztecanthidium*, and other *Dianthidium* by the presence of an elongate apical process medially on T7 well exceeding lateral processes when these are present (Figs. 1–6), and large medial transverse ridge along S3 (Figs. 7–9). Females of *Mecanthidium* differ from *Aztecanthidium* and other *Dianthidium* in the straight cutting edge of the mandible without teeth and without a preapical notch.

Remarks.—*Mecanthidium* was originally placed in the genus *Paranthidium* (Michener 1942), and later transferred to *Dianthidium* (Griswold and Michener 1988) based on the following shared synapomorphies: 1) felt-like setal patches present on the posterior margin of the metanotum lateral to the metanotal pit; 2) scutum with transverse anterior crest or angle separating its vertical anterior margin from the horizontal dorsal surface; 3) pronotum lacking a horizontal dorsal surface; 4) tegula as wide as long, with the widest point behind the middle of the tegula; and 5) the impunctate tergal margins ending at the side of the metasoma. The felt-like setal patches and transverse anterior crest in *Mecanthidium* are not as well developed as in other *Dianthidium*.

KEY TO SPECIES

1. Males 2
- Females 4
2. T7 with apical process short, approximately ½ the total length of tergum (Figs. 3, 5); penis valves not concave apically, not forming opening (Figs. 12, 14) 3
- T7 with apical process long, fingerlike, length much greater than ½ the total length of tergum (Fig. 1); penis valves concave apically forming distinct opening (Fig. 10) ..... ***macrurum* Cockerell**
3. S3 with large, impunctate, transverse process situated medially, anterior surface of process concave and vertical as seen in profile (Fig. 8); medial process of T7 bifurcate (Fig. 3) ..... ***snellingi* sp. nov.**
- S3 with small, punctate, transverse process, anterior surface oblique as seen in profile (Fig. 9); medial process of T7 truncate (Fig. 5) ..... ***zapotecum* sp. nov.**
4. Dorsal margin of preomaular area concave; lateral margin of axilla extending beyond line created by scutum and scutellum ..... ***zapotecum* sp. nov.**
- Dorsal margin of preomaular area not concave; lateral margin of axilla forming contiguous line with scutum and scutellum ..... ***macrurum* Cockerell**



Figs 1–6. Male T7 of *Dianthidium* (*Mecanthidium*) in dorsal (1, 3, 5) and lateral (2, 4, 6) views. *D. macrurum*: 1, 2; *D. snellingi*: 3, 4; *D. zapotecum*: 5, 6.

Dianthidium macrurum Cockerell

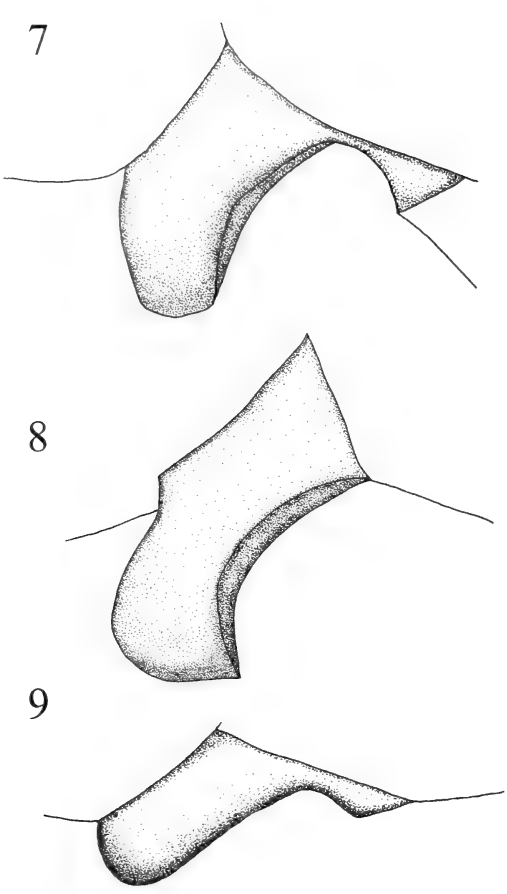
Dianthidium macrurum Cockerell 1913. Annals and Magazine of Natural History 8(xii): 107. Holotype male, Mexico (NMNH, #16226).

Paranthidium (*Mecanthidium*) *sonorum* Michener 1942. Journal New York Entomological Society 50: 278. Holotype male, Mexico, Sonora, Estrella (CASC, #06682). **NEW SYNONYMY**

Diagnosis.—*Dianthidium macrurum* is readily identified by the greatly elongate medial process extending from T7, with a dorsal carina running along the length of the tergum (Figs 1–2). In lateral view, the penis valve appears broad or swollen apically. The apical interior margin of the penis valve is concave forming a pit located anteriorly (Fig. 10).

Distribution.—Central Mexico, the states of Colima, Michoacan, Morelos, Nayarit, Puebla, and Zacatecas.

Material examined.—Mexico: *Colima*: Colima, 33 km NW, 800 m, 4 ♀, on *Cuphea paucipetala*,



Figs 7–9. Male S3 of *Dianthidium* (*Mecanthidium*) in lateral view. 7. *D. macrurum*. 8. *D. snellingi*. 9. *D. zapotecum*.

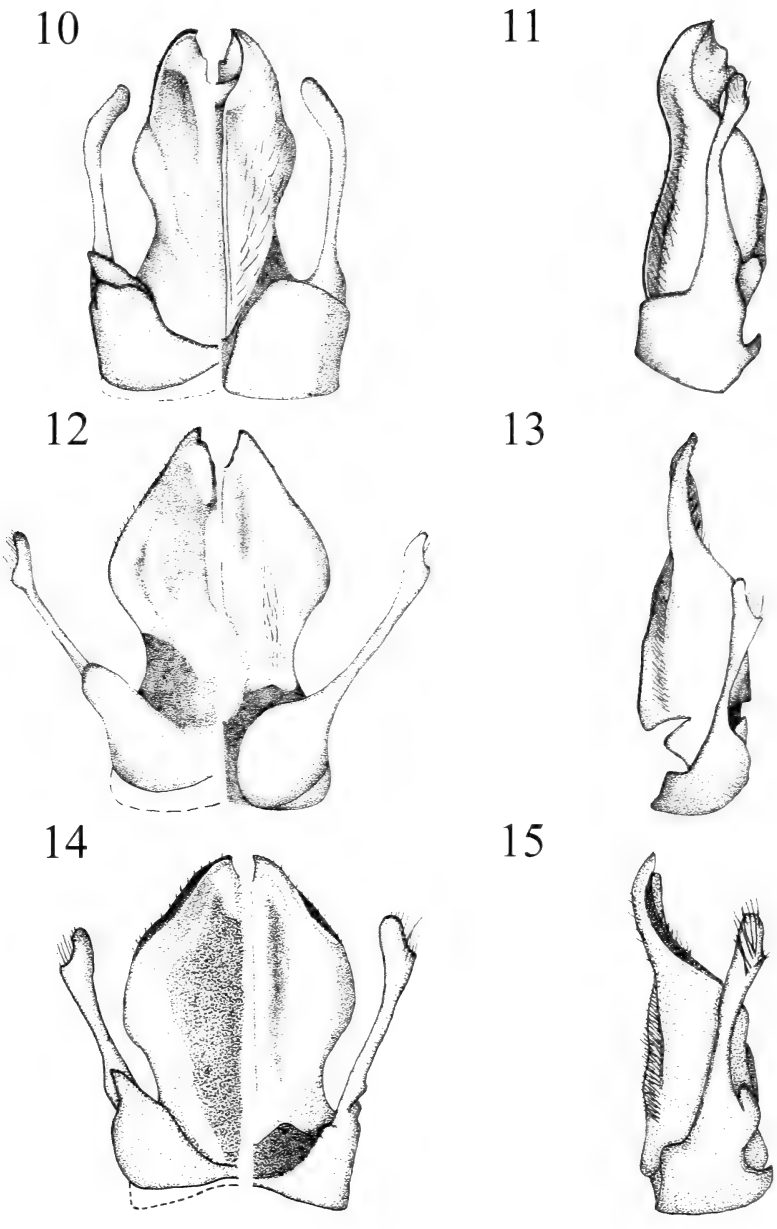
19.Jul.1989, T. Griswold (BBSL); *Jalisco*: Guadalajara, 2 ♀, 3 ♂, Crawford (LACM); Guadalajara, 1 ♂, McConnell (LACM); Guadalajara, 1 ♂, 15.Aug.1976, W. Hanson and M. Schwartz (BBSL); Guadalajara, 1 ♀, 2.Oct.1966, G.E. Bohart and A.S. Bohart (BBSL); Guadalajara, 10 mi N, 2 ♂, 16.Oct.1968, G.E. Bohart (BBSL); Guadalajara, 15 mi NE, 1 ♀ and 2 ♂, 17.Sep.1970, R.M. Bohart and G.E. Bohart (BBSL); Jocotopeca, 3.4 km SE, 1493 m, 1 ♀, on *Cuphea procumbens*, 12.Sep.1976, C.D. George and R.R. Snelling (BBSL); La Floresta, Lago de Chapala, 1510 m, 2 ♂, 4.Sep.1977, E. Schlinger (BBSL); La Floresta, Lago de Chapala, 1510 m, 2 ♀, 4–5.Sep.1977, E. Schlinger (BBSL); Tecolotlan, 5.5 mi NE, 1 ♀, 13.Sep.1982, D.K. Faulkner (LACM); Tequila, 7 km NW, 1275 m, 1 ♀, 10.Sep.1974, E.M. Fisher (LACM); Tizapan *El Alto*, 9 km W, 1585 m, 12.Sep.1976, C.D. George and R.R. Snelling (LACM); *Michoacan*: Huacana, 6 km S, 600 m, 1 ♀, 30 Oct. 1987, T. Griswold; *Morelos*: Cuernavaca, 1 ♂, 8.Nov.–6.Dec. 1987, F.D. Parker (BBSL); Cuernavaca, 6 mi E, 1 ♀, 1.Sep.1974, G. Bohart, W. Hanson (BBSL); Cuernavaca, 10 mi E, 3 males, 15.Sep.1972, W.J. Hanson and J.M. Poff; Yautepec, 1 ♀ and 1 ♂, 13.Sep.1963, F.D. Parker and L.D. Strange; *Nayarit*: Ahuacatlan, 1 ♀, 14.Sep.1970, G.E. Bohart and R.M. Bohart (BBSL); Ixtlan del Rio, 7 mi W, 1 ♂, 10.Sep.1970, E.M. Fischer (LACM); Ixtlan del Rio, 1 ♂, 10.Sep.1970, E.M. Fischer (LACM); *Puebla*: Izucar de Matamores, 9 mi W, 2 ♀ and 1 ♂, 16.Sep.1972, W.J. Hanson and J.M. Poff (BBSL); *Zacatecas*: Jalpa, 10 mi S, 1 ♂, 17.Sep.1970, G.E. Bohart and R.M. Bohart (BBSL).

Variation.—S3 in *D. macrurum* has a transverse medial process that varies in size with the size of the specimen. Large individuals have a transverse process that is taller than ½ the length of the sternum, while the height of the sternal process of small bees is considerably less than ½ its length.

Comments.—Comparison of numerous male and female specimens of putative *D. macrurum* and *D. sonorum* failed to yield characters that justify separate specific designations. The key character thought to distinguish *D. macrurum* from *D. sonorum* was the prominence of S3 (Fig. 2). A review of additional material shows a continuum in size in this structure between individuals identified as *D. macrurum* and *D. sonorum*. We find no difference in male genitalia, while there are distinct differences among other *Mecanthidium* species. Additionally, there is considerable overlap in the geographic distribution between *D. macrurum* and *D. sonorum*.

Dianthidium snellingi Tanner and Griswold, sp. nov.

Diagnosis.—The male of *D. snellingi* is readily identifiable by the following combination of characters: 1) a diminutive projection at the apex of T7 (Figs 3–4), and 2) a large transverse ridge across S3 (Fig. 8). The projection on the tip of T7 is broadly bifurcated and the lateral margins



Figs 10–15. Genitalia of *Dianthidium* (*Mecanthidium*) in dorsal (left half) and ventral (right half) views (10, 12, 14) and lateral profile (11, 13, 15). *D. macrurum*: 10, 11. *D. snellingi*: 12, 13. *D. zapotecum*: 14, 15.

of the tergum are broadly rounded. The anterior face of the ridge across S3 is concave, giving the distal margin the appearance of being broader than its base in lateral view. Other characters useful in identifying *D. snellingi* are: 1) penis valve in lateral view with apex narrow (Figs 12–13), 2) the interior apical margin of the penis valve is not concave, without an anterior pit.

Male.—Color and pubescence: Face uniformly covered in simple reddish-brown setae except paraocular area; hypostomal area with long, dense, plumose setae. Vertex, genal area, and integument of paraocular area reddish-brown to light

orange. Integument of supraclypeal area, frons, and ocellar area black except small reddish-brown marks dorsal to clypeus, between antennal sockets and ventral to median ocellus. Clypeus with yellow integument apically, reddish-brown basally, apical margin black; setae longer along clypeal margin. Mandible orange with black ventral, dorsal, and cutting margins. Scape, pedicel, and first two flagellar segments of antenna mostly reddish-brown; remaining segments mostly black. Scape densely setose on basal ½. Gena densely setose with plumose setae. Integument of mesosoma mostly reddish-brown except propodeum black, and scutum with black triangle at anterior margin with apex pointing posteriorly, and thick black longitudinal sublateral marking. Scutum covered in short dense setae. Wings heavily infuscated throughout. Legs brightly reddish-brown with black markings on fore femur and on distal margins of fore tibia. Tarsi mostly orange with dense reddish-brown setae. Integument of metasoma mostly reddish-brown, T2–T7 with narrow black basal marks, dorsum covered in short decumbent orange setae. S3–S6 densely covered with long, simple, orange setae. Anterior face of transverse process with sparse orange setae. S3–S4 with long dense apical fringes.

Head.—Mandible tridentate, medial tooth low, truncate, nearer ventral than dorsal tooth. Clypeus in lateral view, distinctly convex, broadest below middle; surface deeply, contiguously punctate; punctures wider than long with dorsal margin of puncture raised making surface of clypeus appear tuberculate; punctures separated by no more than ½ × puncture width; apical margin truncate, irregularly tuberculate. Juxtantennal ridge reduced to inconspicuous angle. Malar space absent. Gena widest dorsally, maximum width approximately eye width. Vertex sharply angulate in lateral view.

Mesosoma.—Pronotal lobe lamellate, anterior margin distinctly convex. Scutum shiny, densely but not contiguously punctate. Punctures on lateral face of mesepisternum larger than elsewhere on mesosoma, not contiguous. Preomaular area distinct, separated from lateral face of mesepisternum by omaular carina in dorsal half. Metepisternum nearly impunctate ventrally. Margin of axilla subangulate ventrally. Propodeum vertical with limited dorsal face; with large glabrous region at its distal margin extending up approximately ½ × length.

Metasoma.—T7 with rounded lateral lobe basally, apically produced into finger-like bifurcated process, with long medial carina extending length of tergum (Fig. 3). S3 with large impunctate transverse process subapically (Fig. 8); thickness in lateral view equal to ½ × length of sternum, apex wider than base in lateral view due to convex anterior face. Genitalia with penis valve not emarginate apically, thus the two valves without a visible apical opening (Fig. 12), in lateral view narrow apically (Fig. 13); gonostylus with concave apical margin, in lateral view comma shaped (Fig. 13).

Female.—Unknown

Holotype male.—MEXICO: *Jalisco*: Mazamitla, 3 mi NE, 12.July.1982, D.K. Faulkner (LACM). Holotype deposited in LACM.

Etymology.—Named in honor of Roy Snelling for his great contribution to Hymenopteran taxonomy.

Distribution.—Known only from Jalisco, Mexico.

Comments.—We consider *D. snellingi* to be a morphologically distinct species from both *D. macrurum* and *D. zapotecum* based on the shape and size of the apical process on T7, the shape and size of the medial process on S3, and the thickness of the apex of the penis valve and gonostylus. *Dianthidium snellingi* has a diminutive apical process relative to *M. macrurum*, and the apex of this process in *D. snellingi* is broadly bifurcated compared to complete in *D. macrurum* and *D. zapotecum* (Figs 1, 3, 5). The medial process of S3 is large

relative to that of *D. zapotecum*, though there may be similar variation in its size, as seen in *D. macrurum*. Also, the anterior face of this process is concave in *D. snellingi*, making the distal margin appear broader than its base in lateral view (Fig. 8). S3 in *D. macurum* is not concave and gradually tapers to its apex in lateral view (Fig. 7). The apex of the penis valve of *D. snellingi* lacks a visible dorsal apical pit, and in lateral view it tapers gradually to its apex. The internal margin of the penis valve of *D. macrurum* is open and concave, exposing a dorsal pit; in lateral view, the apex of the penis valve is broad or swollen. The gonostylus of *D. snellingi* is most narrow at 1/3 of its length, in lateral view, but it lacks a basal lobe. The gonostylus of *D. zapotecum* also narrows significantly at 1/3 its apex, but has a prominent basal lobe.

Dianthidium zapotecum Tanner and Griswold, n. sp.

Diagnosis.—Males of *D. zapotecum* are easily recognized by having a diminutive apical projection on T7 (Figs 5–6) and a diminutive process on S3 (Fig. 9). T7 has obtusely angulate lateral projections and the apex of the medial process is entire. The transverse process on S3 is much smaller than that of *D. macrurum* and *D. snellingi*; its thickness in lateral view is approximately equal to ¼ the length of the sternum. Other diagnostic characters include: penis valve with apex in lateral view narrow (Figs 14–15); interior apical margin of the penis valve not concave, without anterior pit. Females of *D. zapotecum* are recognizable by the combination of a concave anterior margin of the preomaular area, and axillae with lateral margins that extend beyond a line created between the lateral margins of the scutum and scutellum. In both sexes, the anterior margin of the pronotal lobe is almost in the same plane as the anterior margin of the scutum.

Male.—Color and pubescence: Face uniformly covered in simple reddish-brown setae except paraocular area; hypostomal area with long, dense, plumose setae. Integument reddish-brown to light orange on vertex, genal area, paraocular area of face. Integument black on supraclypeal area, frons, ocellar area except small reddish-brown marks dorsal to clypeus, between antennal sockets and ventral to median ocellus. Clypeus yellow to orange with sparse long yellow setae, setae longer along black clypeal margin. Mandible orange with black ventral, dorsal, and cutting edge margins. Scape, pedicel, first two flagellar segments of antenna orange, remaining segments mostly brown. Scape setose with plumose setae on basal half. Gena densely setose with plumose setae. Scutum covered in short dense plumose setae, integument with black stripe at anterior margin extending longitudinally to middle, and small black mark anterior of axilla. Integument of axilla, scutellum reddish-brown, rest of mesosoma black to dark brown except for marginal ferrugious markings on the mesepisternum. Wings infuscated throughout. Integument of legs brightly reddish-brown with black markings on hind tibia. Tarsi mostly orange with dense reddish-brown setae. Integument of metasoma mostly reddish-brown, T2–T7 with black to dark brown basal and apical bands, dorsum covered in short decumbent orange setae. T1–T5 with medial longitudinal dark to light brown integumental stripe. S3 with anterior face of medial transverse projection with sparse orange setae. S4–S6 with plumose, silver setae, dense apical band of long, simple, silver setae.

Head.—Mandible tridentate, medial tooth angulate, nearer ventral than dorsal tooth. Clypeus deeply, densely punctate, punctures separated by no more than ½ × width of puncture, as wide as long, dorsal margin of puncture raised making surface of clypeus appear tuberculate, apical margin truncate, irregularly tuberculate. Juxtantennal ridge produced into tooth. Malar space absent. Gena widest dorsally, maxi-

mum width approximately ½ eye width. Preoccipital margin angulate in lateral view.

Mesosoma.—Pronotal lobe punctures less dense than on rest of mesosoma, not contiguous; anterior margin almost on same plane as anterior margin of scutum. Mesepisternum with distinct anterior face, separated from lateral face by carina. Outer margin of axilla subangulate posteriorly. Propodeum vertical with narrow dorsal face, with large glabrous region at its distal margin extending up approximately ½ × length.

Metasoma.—T7 with long medial carina, with lateral rounded projection (Fig. 5). S3 with small punctate transverse process situated medially; height equal to ¼ × length of sternum.

Female.—Color and pubescence: Face uniformly covered in simple yellow setae. Integument of vertex and genal area reddish-brown, paraocular area dorsally reddish-brown to yellow anteriorly. Integument of supraclypeal area, frons, and ocellar area black except quadrate reddish-brown mark between antennae and reddish-brown longitudinal band from median ocellus. Clypeus reddish-brown basally, yellow apically. Mandible reddish-brown with black ventral, dorsal, and cutting margins. Scape, pedicel, and first two flagellar segments of antenna reddish-brown; remaining segments mostly brown. Integument of scutum reddish-brown with variable black markings, frequently with central longitudinal band, lateral black band. Integument of axilla, scutellum reddish-brown, rest of mesosoma black to dark brown except for marginal ferruginous markings on mesepisternum. Wings heavily infuscated throughout. Legs brightly reddish-brown with black markings on hind tibia. Tarsi mostly yellow with dense reddish-brown setae. Integument of mesosoma mostly reddish-brown, segments T2–T7 with narrow black to dark brown basal and apical bands, dorsum covered in short decumbent tawny setae. S2–S4 with black basal bands.

Head.—Mandible edentate, apical margin with slight incurve near ventral angle, acute angle dorsally. Clypeus in lateral view distinctly convex, broadest below middle; surface deeply, contiguously, punctate; punctures as wide as long, with dorsal margin of punctures raised making surface of clypeus appear tuberculate; apical margin truncate, irregularly tuberculate. Punctures separated by as much as one puncture width. Scape uniformly covered in simple short setae. Juxtantennal ridge reduced to inconspicuous angle. Malar space absent. Gena widest dorsally, maximum width approximately eye width; densely setose with plumose setae. Vertex sharply angulate in lateral view.

Mesosoma.—Scutum punctate, covered in short, dense, stout, setae. Punctures on lateral face of mesepisternum larger than elsewhere on mesosoma, not contiguous, nearly impunctate below. Preomaular area with distinct anterior face, separated from lateral face by omaular carina on dorsal half. Outer margin of axilla subangulate laterally. Propodeum vertical with limited dorsal face; with large glabrous region distally extending approximately half length of segment.

Metasoma.—Scopa composed of long simple setae spanning S2–S5.

Distribution.—Mexico in the states of Chiapas and Oaxaca.

Type material.—HOLOTYPE: ♂, MEXICO: *Oaxaca*: El Camaron, 20 mi E, 21.Jul.1956, J.W. MacSwain. PARATYPES: MEXICO: *Oaxaca*: Cuicatlan, 4 mi N, 4900', 1 ♂, 18.Jul.1973, R.R. Snelling; Tehuantepec, 8 km W, 3 ♀, 9–10.Aug.1974, E.M. Fisher and J.L. Fisher; *Chiapas*: El Aquacero, nr Ocozocoautla, 1 ♀, 26.Oct.1986, E. Fischer and D. Thomas; 1 ♀, Tuxtla Gutierrez, 26.Jul.1987, F.D. Parker. Holotype deposited in CISC; paratypes deposited in BBSL, CISC, and LACM.

Variation.—Males vary in integumental color, particularly on the mesosoma which varies from tawny to dark reddish-brown.

There is also some variation in the color of the mandibles from light tawny to orange, and the size and position of the black integumental markings of the scutum. There seems to be little variation, however, in the size and shape of the apical process of T7 and the medial process of S3. Females also vary in integumental color, most notably on the mesosoma. Individuals with dark mesosoma appear to have darker and more robust medial bands on the terga.

Comments.—Dianthidium zapotecum is morphologically distinct from both *D. macrurum* and *D. snellingi* in the shape and size of the apical process on T7, the shape and size of the medial process on S3, and the thickness of the apex of the penis valve and gonostylus. The apical process on T7 of *D. zapotecum* is diminutive relative to other *Mecanthidium* and the apex does not bifurcate, as it does in *D. snellingi*. In lateral view the anterior face of the process is not concave, as in *D. snellingi*, and does not taper, as in *D. macrurum*. The penis valve of *D. zapotecum* is not swollen, as in *D. macrurum*, and the gonostylus has a basal lobe that is absent in *D. snellingi*. The geographical distribution of *D. zapotecum* appears to be disparate from either *D. macrurum* or *D. snellingi*. *Dianthidium macrurum* is distributed across central Mexico from the western coastal states of Colima, Michoacan, and Nayarit to the central states of Puebla and Zacatecas. *Dianthidium snellingi* has been collected in the center of this distribution in the western coastal state of Jalisco. *Dianthidium zapotecum* is only known from the southern states of Oaxaca and Chiapas.

ACKNOWLEDGMENTS

We would like to acknowledge Joseph Wilson, Kevin Williams, and Victor Gonzalez for thoughtful reviews of this manuscript; Frank Parker and. Ricardo Ayala for providing recent material. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, UT and was approved as journal paper no. 8098

LITERATURE CITED

Cockerell, T. D. A. 1913. Descriptions and records of bees. LIII. *Annals and Magazine of Natural History* 8: 103–110.

Griswold, T. L. and C. D. Michener. 1988. Taxonomic observations on Anthidiini of the western hemisphere (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 61: 22–45.

Michener, C. D. 1942. Taxonomic observations on bees with descriptions of new genera and species (Hymenoptera: Apoidea). *Journal of the New York Entomological Society* 50: 273–282.

———. 2007. *The Bees of the World*. 2nd Edition. Johns Hopkins University Press, Baltimore, Maryland.

Parker, F. D. 1977. Biological notes on some Mexican bees. *Pan-Pacific Entomologist* 53: 189–192.

J. HYM. RES.
Vol. 18(2), 2009, pp. 192–204

Review of *Acanthophotopsis* Schuster (Hymenoptera: Mutillidae)

David A. Tanner, Nicole F. Boehme and James P. Pitts*

Department of Biology, Utah State University, Logan, UT 84322, USA

Abstract.—***Acanthophotopsis snellingi* Tanner and Pitts, sp. nov.**, is described based on males collected from Chihuahua and Fresnillo, Mexico, which raises the number of species of *Acanthophotopsis* to six. *Acanthophotopsis snellingi* differs from other species of *Acanthophotopsis* by having the following unique combination of characters: the head is elongate, with the lateral margin parallel behind the eyes and converging posteriorly; the basal margin of the clypeus lacks a median longitudinal carina and central tubercle; the mandible is tridentate; and the first flagellar segment is 1.5–2× long as wide. We also report that *A. falciformis furcisterna* is a **junior synonym** of *A. falciformis falciformis*. An illustrated key is given for the species of *Acanthophotopsis*.

Key words.—Nocturnal, Sphaeropthalminae, velvet ant, Nearctic Deserts

Acanthophotopsis Schuster (Hymenoptera: Mutillidae), which belongs to the subfamily Sphaeropthalminae (Brothers 1975; Schuster 1958), is a poorly understood genus of nocturnal velvet ants that is endemic to southwestern North America and known only from males. The natural history of many Sphaeropthalminae, including *Acanthophotopsis*, is poorly known. It is assumed that, similar to other Nearctic Sphaeropthalminae, they are parasitic on spheciform wasps and solitary ground nesting bees (Krombein et al. 1979).

Schuster (1958) described *Acanthophotopsis* with two other genera, *Acrophotopsis* and *Dilophotopsis*. Although these other genera have been treated recently (Pitts and McHugh 2002; Wilson and Pitts 2008), *Acanthophotopsis* has yet to be reviewed. At its description, *Acanthophotopsis* included five species and two subspecies. These species range from the palm desert region of California, east to Oklahoma, and south into the arid Northern regions of Mexico. Species of *Acanthophotopsis* are medium-sized and are largely reddish-brown with pale white setae throughout the body. At first glance they look like many other nocturnal mutillid genera. This genus, however, can be easily distinguished from other Nearctic sphaeropthalmines by the presences of large mesosternal processes that are conical apically and are directed slightly posteriorly, and by a swollen middle tibia with only a single tibial spur.

Species of this genus are rare in collections. In a study of over 20,000 specimens of nocturnal mutillids from museums throughout the Southwest, only a handful of specimens of each *Acanthophotopsis* species was found, except for *A. falciformis* Schuster. This latter species is found primarily in the USA, while the remaining species of *Acanthophotopsis* range into northern Mexico. The rarity of these species in collections may be due to the difficulty of collecting in Mexico, rather than a true reflection of their natural abundance.

In the course of our studies, we found an undescribed species of *Acanthophotopsis*. We describe this new species and report a new synonymy of the subspecies *A. falciformis falciformis* and *A. falciformis furcisterna*.

* Author for correspondence

MATERIALS AND METHODS

The following acronyms are for institutions or collections housing the material discussed in the current study:

AEIC	American Entomological Institute, Gainesville, Florida, USA.
AMNH	American Museum of Natural History, New York, New York, USA.
BYUC	Entomology Section, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA.
CASC	California Academy of Sciences, San Francisco, California, USA.
CISC	Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, California, USA.
EMUS	Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.
KAWC	Kevin A. Williams Personal Collection, Utah State University, Logan, Utah, USA.
NMNH	National Museum of Natural History, Washington, D.C., USA.
NVDA	Nevada State Department of Agriculture, Reno, Nevada, USA.
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.
UAIC	Department of Entomology Collection, University of Arizona, Tucson, Arizona, USA.
UCDC	The Bohart Museum of Entomology, University of California, Davis, California, USA.
UCRC	UCR Entomological Teaching and Research Collection, University of California, Riverside, California, USA.
UMSP	University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

We adopt the following notation for punctures in the order of decreasing coarseness: reticulate, coarse, moderate, small, fine and micropunctate (Ferguson 1967). Micropunctate punctures are extremely shallow and do not have vertical walls or sharp margins. Fine refers to shallow punctures that have slanted or curved walls and are separated by greater than 10× their width. Small punctures have slightly vertical walls and are separated by 2–10× their diameter. Moderate refers to punctures that tend to be circular, are separated by 0.5–2× their width, and have curved to vertical walls. Coarse refers to punctures that are closely spaced (0.2–0.5× puncture width) with vertical walls and punctures are usually circular. Reticulate refers to sculpturing that resembles a network of lines with the punctures closely spaced (<0.2 puncture width) with vertical walls. "Simple setae" are setae that are smooth and do not have barbed surfaces. "Brachyplumose setae" are setae with barbs that are less than, or equal to, the diameter of the shaft at the attachment of the barb. "Plumose setae" have longer barbs. We use "tibial spurs" instead of "calcaria" and "paramere" instead of "gonoforcep". The acronyms T2, T3, etc., denote the second, third, etc., metasomal tergites, respectively. Similarly, S2, S3, etc., signifies the second, third, etc., metasomal sternites, and F2, F3, etc., signify the second and third flagellar segments of the antenna, respectively. In the material examined section, an asterisk denotes the specimen which was used to illustrate the genitalia.

Acanthophotopsis Schuster

Acanthophotopsis Schuster, 1958. Ent. Amer. (n. s.) 37: 5 (in key), 88. Type-species: *Acanthophotopsis falciformis* Schuster, Orig. desig.

Male diagnosis.—*Acanthophotopsis* is distinguishable from other nocturnal velvet ants by the large mesosternal processes that are conical apically, slightly directed

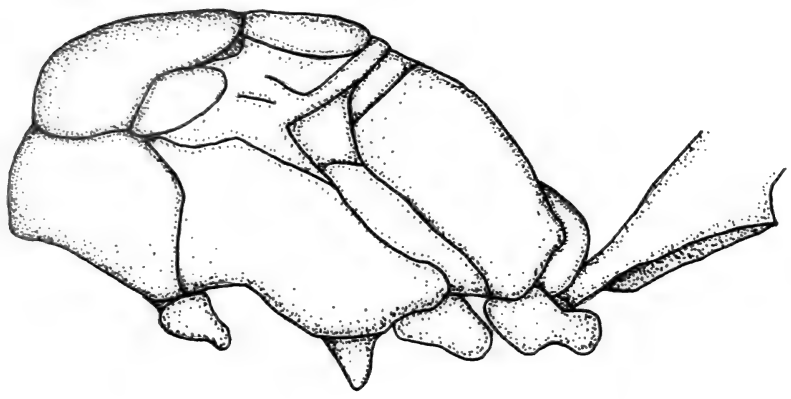


Fig. 1. Mesosoma of *Acanthophotopsis snellingi*. Mesosternal process located anterior to the mesosternal coxae.

posteriorly and easily viewed without a microscope (Fig. 1), and the swollen middle tibia with a single mid-tibial spur. Other characters useful in identifying *Acanthophotopsis* include the ventral tooth of the mandible being small and angulate to slightly rounded, or absent, and followed by a slight emargination. Also, the hypopygidium is unmodified lacking lateral carinae. The parameres are short and stout (Figs 14–19), and have apices that do not overlap *in situ*. The cuspis of the genitalia is densely setose and often curled and spatulate at the extreme apex (Figs 14–19). Lastly, the apical margins of the metasomal segments have sparse setae on the fringes that are at the transition of being termed plumose or brachyplumose.

Females.—Unknown.

Remarks.—We have encountered some specimens of *Acanthophotopsis* that have two mid-tibial spurs, though this condition is rare. Specimens that have a second mid-tibial spur also have a swollen mid-tibia and conical mesosternal processes and are, therefore, still distinguishable from the other North American nocturnal velvet ants. Also, these specimens typically have two mid-tibial spurs on only one leg rather than on both.

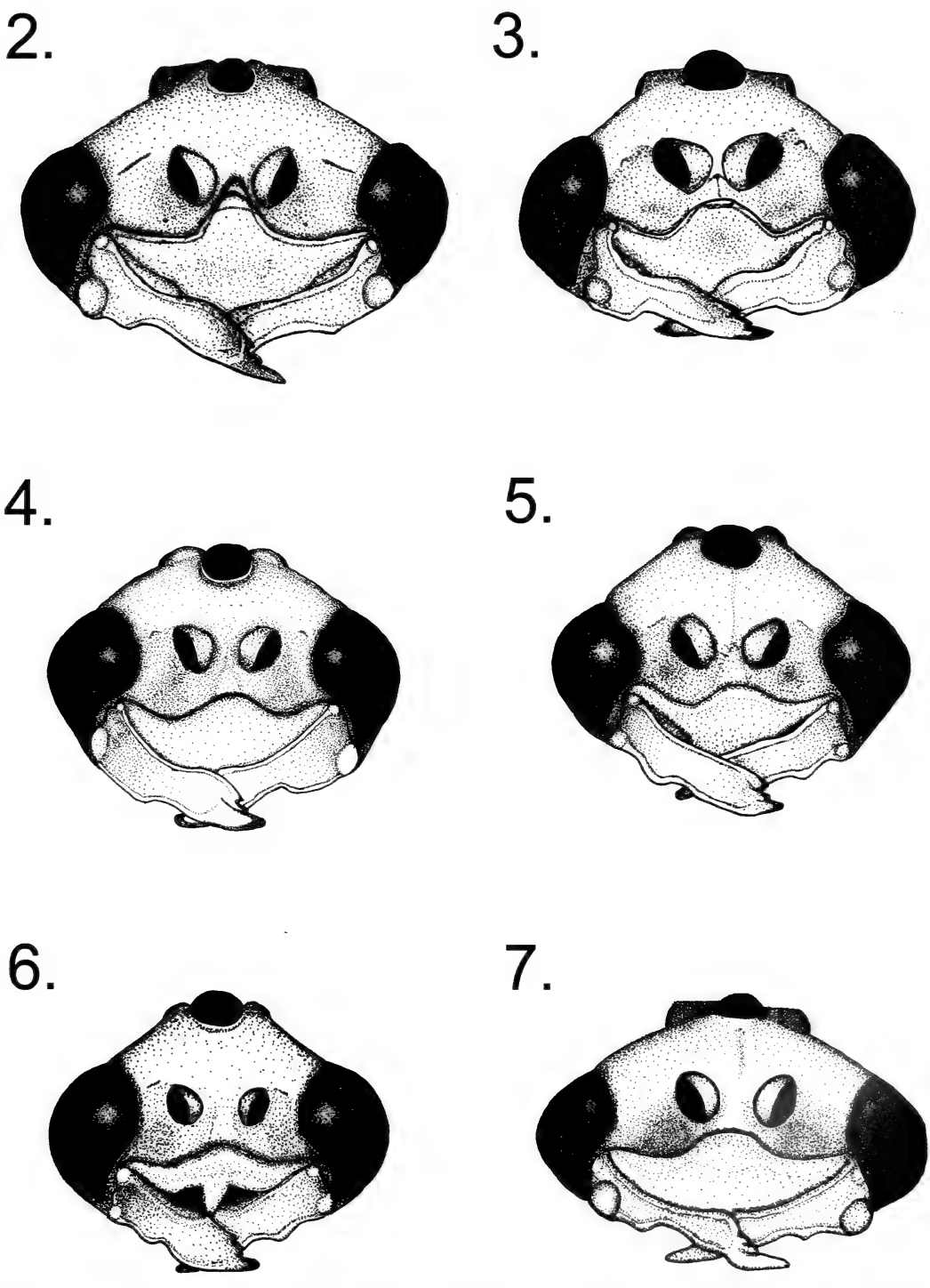
Schuster (1958), when describing *Acanthophotopsis*, also described two species-groups: the *A. falciformis* species-group, which consisted of the two subspecies of *A. falciformis*, and the *A. dorophora* species-group, which includes the remaining four species. We dispense with species-groups in this manuscript because of the small size of the genus, the evidence suggesting that *A. falciformis furcisterna* is a junior synonym of *A. falciformis falciformis*, and because the genus is clearly a homogenous group.

The females of this genus are unknown. Based on unpublished molecular data (ITS1 and ITS2), this genus is closely related to the *Sphaeropthalma blakeii*, *S. baboquivari*, and *S. papaga* species-groups; therefore, the female will likely be similar to the females of these groups.

Acanthophotopsis bequaertii Schuster

Acanthophotopsis bequaertii Schuster, 1958. Ent. Amer. (n. s.) 37: 12 (in key), 101. male. Holotype: Arizona, Hereford, 16.Sep.1935, coll. F.H. Parker (UMIC).

Male diagnosis.—*Acanthophotopsis bequaertii* is identified by the following unique combination of characters: the mandibles are tridentate, and the dorsal carina of the mandible ends before the apex, such that the apex of the mandible appears to be oblique (Fig. 2). The base of the clypeus is distinctly raised and transversely carinate, but lacks a central tubercle and is not horizontally produced. The head behind



Figs 2–7. Face of *Acanthophotopsis bequaertii* (2), *A. bifurca* (3), *A. dorophora* (4), *A. evansii* (5), *A. falciformis* (6), and *A. snellingi* (7).

the eyes is elongate with the margins directly posterior to the eyes nearly parallel for a distance equal to one half the length of the eye (Fig. 8). Other characters useful in identifying *A. bequaertii* are: 1) the frons is coarsely punctate while the vertex is moderately punctate, 2) the length of F1 is 1.75× its width, 3) the length of the stigma is nearly equal to the length of the marginal cell along the costa, and 4) the paramere in lateral view is equally broad throughout its length except for the apex, which narrows to an acute angle, and is 4× as broad as the cuspis medially (Fig. 14).

Material examined.—**USA: Arizona**, *Cochise Co.*: 5 mi E Hereford, 1 ♂, 2.Jun.1966, coll. R.F. Sternitzky (EMUS); Portal, 1 mi. S, 1 ♂, 16.Aug.1966, coll. E.G. and J.M. Linsley (CISC), 3 ♂, 25.Aug.1964, coll. J.H. Puckle, M.A. Mortenson, and M.A. Cazier (CISC); Cave Cr. Ranch, 1 ♂, 10.Aug.1969, coll. E.G. Linsley (CISC); Sierra Vista, 1 ♂, 21.Oct.1961, coll. R.F. Sternitzky (EMUS); Sonoita, 1 ♂, 13.Jul.1966, coll. R. Hennessey (CISC); *Santa Cruz* Co.: Canelo, 1 ♂*, 21.Jun.1958, coll. G.D. Butler (UAIC); Parker Canyon Lake, SW slope Huachuca Mts, 12–13.Aug.1968, coll. F. Werner (UAIC). **MEXICO: Chihuahua**: Carmargo, 25 mi SW, 1 ♂, 14.Jul.1947, coll. D. Rockefeller Exp. Schramel (AMNH); Camargo, 42 mi SW, 4900', 3 ♂, 5.Jul.1947, coll. D. Rockefeller Exp. Schramel (AMNH); Santa Barbara, 5500', 1 ♂, 20.Jul.1947, coll. D. Rockefeller Exp. Schramel (AMNH). **Durango:** San Juan del Rio, 5200', 1 ♂, 30.Jul.1947, coll. D. Rockefeller Exp. Schramel (AMNH); Encino, 6200', 1 ♂, 27.Jul.1947, coll. D. Rockefeller Exp. Schramel (AMNH).

Remarks.—Previously, this species was only known from the holotype. This species is most likely to be confused with *A. bifurca* (Fig. 15) due to the similarities in the presences of a medial tubercle on the clypeus and the lack of a complete dorsal carina on the mandible, such that the apex of the mandible is not vertical as in the other *Acanthophotopsis* species. The genitalia of these two species differ. The paramere of *A. bequaertii* (Fig. 14) is thicker and the apex of the cuspis is more obviously lobed.

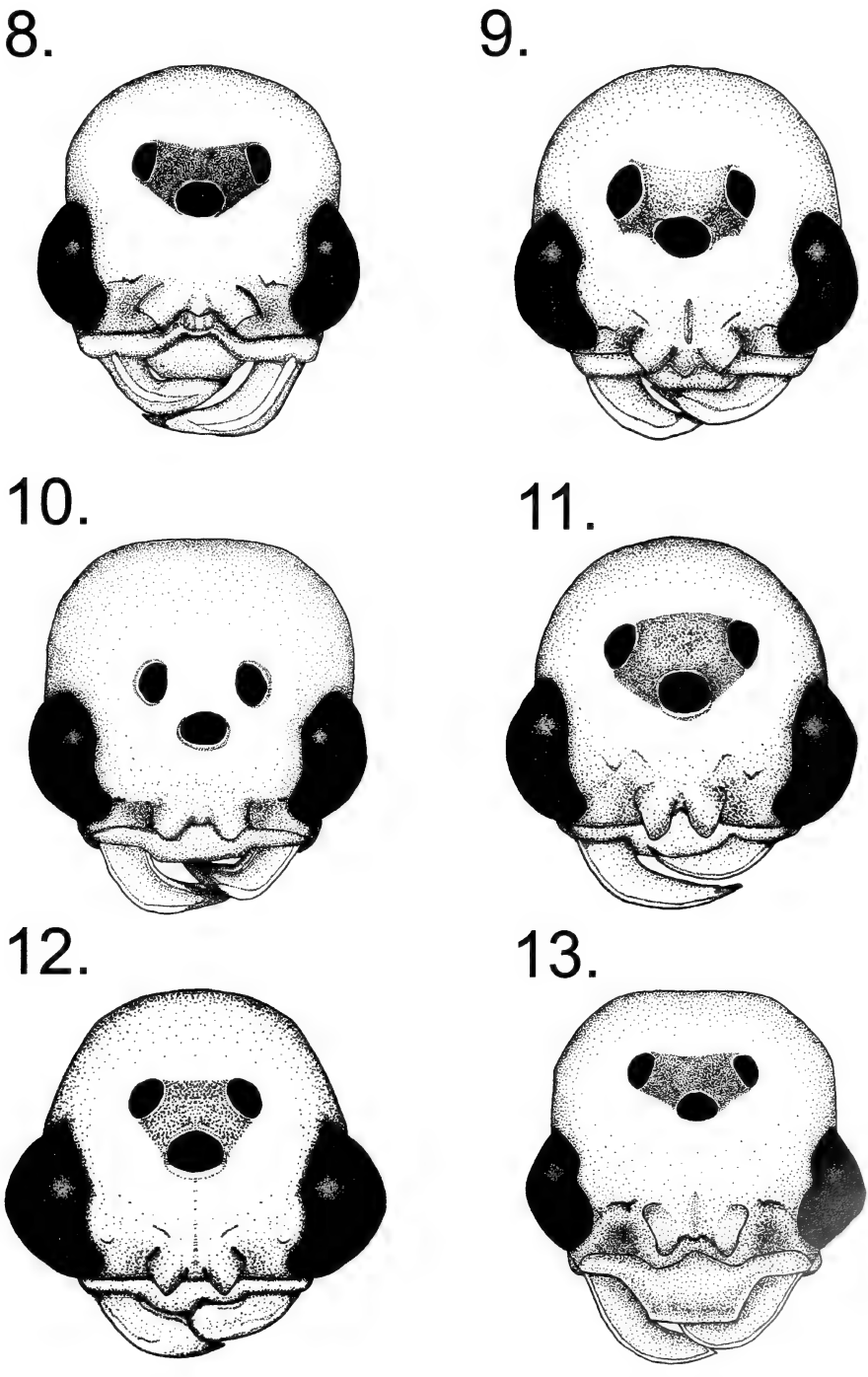
Acanthophotopsis bifurca Schuster

Acanthophotopsis bifurca Schuster, 1958. Ent. Amer. (n. s.) 37: 13 (in key), 98. male. Holotype: Texas, Winterhaven, 15.May.1935, coll. S.E. Jones (UMIC).

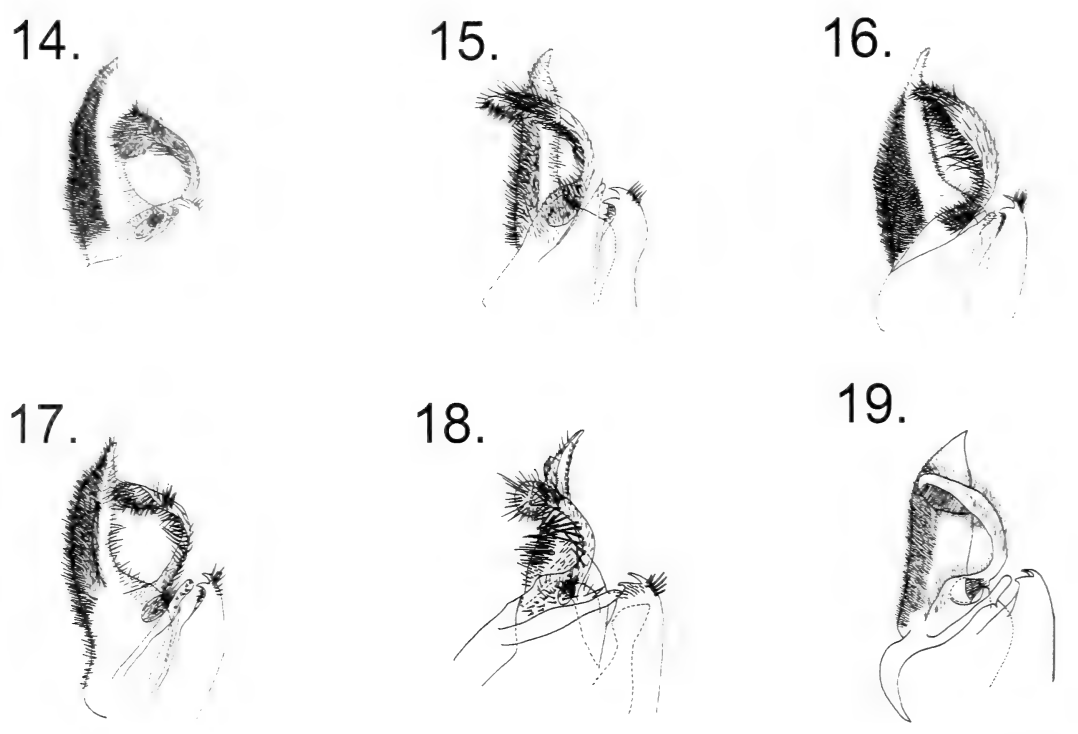
Male diagnosis.—*Acanthophotopsis bifurca* is identified by the following unique combination of characters. The mandibles are tridentate and the dorsal carina of the mandible ends before the apex of the mandible, such that the apex of the mandible appears to be oblique (Fig. 3). The base of the clypeus is raised into a slight transverse median tubercle, but the anterior portion of the clypeus not horizontally produced. The head behind the eye is convergent giving the head a rounded appearance (Fig. 9). Other characters useful in identifying *A. bifurca* are: 1) the frons is coarsely punctate while the vertex is moderately punctate, 2) the length of F1 is 2× its width, 3) the length of the stigma is 0.75× the length of the marginal cell along the costa, and 4) the paramere in lateral view is equally broad throughout its length except for the apex, which narrows to an acute angle, and the paramere is 2–3× as broad as the cuspis medially (Fig. 15).

Material examined. **USA: Oklahoma**, *Kiowa Co.*, Lugert, 1 ♂, 11.Jun.1937, coll. Standish-Kaiser (UAIC). **New Mexico**, *Eddy Co.*, 1 ♂, 12.Jul.1927, coll. R.H. Beamer (SMEC). **Texas**, *Val Verde Co.*: 1 ♂*, 6.May.1941, coll. D.J. and J.N. Knull (UMSP); Del Rio, 2 ♂, 25.Apr.1959, coll. W.R.M. Mason (EMUS); 1 ♂, 10.Sep.1976, coll. J.A. Powell and J.A. Chemsak (CISC); *Kinney Co.*, Brackettville, 1 ♂, 4.May.1950 (CISC).

Remarks.—Previously, this species was only known from the holotype and two paratypes. We were unable to locate the two paratypes. This species would most likely be confused with *A. bequaertii*; see the discussion in the remarks section for *A. bequaertii* for characters useful in distinguishing these two species.



Figs 8–13. Frontal view of head of *Acanthophotopsis bequaertii* (8), *A. bifurca* (9), *A. dorophora* (10), *A. evansii* (11), *A. falciformis* (12), and *A. snellingi* (13).



Figs. 14–19. Genitalia, lateral view, *Acanthophotopsis bequaertii* (14), *A. bifurca* (15), *A. dorophora* (16), *A. evansii* (17), *A. falciformis* (18), and *A. snellingi* (19).

Acanthophotopsis dorophora Schuster

Acanthophotopsis dorophora Schuster, 1958. Ent. Amer. (n. s.) 37: 13 (in key), 104. male. Holotype: Arizona, Tucson, 26.Aug.1935, coll. O. Bryant (UMIC).

Male diagnosis.—*Acanthophotopsis dorophora* is identified by the following set of unique characteristics: the mandibles are tridentate and the dorsal carina of the mandible is complete, reaching from the base of the mandible to the innermost tooth, and the apex of the mandible is vertical apically (Fig. 4). Although the surface of the clypeus just anterior to its base is slightly raised, it lacks a median tubercle or transverse carina. The clypeus is horizontally produced, or plate-like. The head behind the eyes is elongate, with the margins of the head just posterior to the eyes almost parallel for a distance equal to one half the length of the eye (Fig. 10). Other characters also useful in identifying *A. dorophora* are: 1) the frons and vertex are coarsely punctate, and the area between the punctures of the vertex is highly polished, 2) the length of F1 is 2.75× its width, 3) the length of the stigma is 0.95× the length of the marginal cell along the costa, and 4) the paramere tapers evenly from the base to the apex, and ends in an acute angle (Fig. 16).

Material examined.—**Arizona**, *Yuma Co.*: Yuma, 1 ♂*, 15.Oct.1958, coll. V. Roth (UAIC); Yuma, 1 paratype ♂, 21.VIII.1930, coll. H.M. Smith (NMNH); 12 mi NE Yuma, Gila River valley, 1 ♂, 29.May.1961, coll. H.F. Howden (EMUS). **California**, *Imperial Co.*, Algodones Dunes: Cahuilla Ranger Sta. 10 km WSW Glamis, 1 ♂, 22.Sep–15.Nov.2008, E. Dreyfus (UCDC); Brawley, 1 ♂, 22.Jun.2004, coll. K.A. Williams (KAWC).

Remarks.—Previously, this species was known from only the holotype. This species could be confused with *A. snellingi*, sp. nov. See the discussion for the latter

species for characters useful in distinguishing these two species.

Acanthophotopsis evansii Schuster

Acanthophotopsis evansii Schuster, 1958. Ent. Amer. (n. s.) 37: 12 (in key), 93. male. Holotype: Mexico, Durango, San Juan Del Rio, 7.Aug.1951, coll. H.E. Evans (CUIC).

Male diagnosis.—*Acanthophotopsis evansii* is identified by the following set of unique characters. The mandibles are tridentate, the dorsal carina of the mandible is complete to the innermost tooth; the apex of the mandible is vertical apically (Fig. 5). The base of the clypeus is slightly raised, but not produced into a carina or a tubercle. The clypeus is only slightly horizontally produced, and not plate-like. The head behind the eyes is strongly convergent (Fig. 11). Other characters useful in identifying *A. evansii* are: 1) the frons of *A. evansii* is coarsely punctate with shallow punctures while the vertex is moderately punctate; 2) the length of F1 is 2.5× its width; 3) the length of the stigma is 0.7× the length of the marginal cell along the costa; 4) the paramere in lateral view is equally broad throughout its length except for the apex, which narrows to an acute angle; and 5) the paramere is 2–3× as broad as the cuspis medially (Fig. 17).

Material examined.—**USA: New Mexico**, *Eddy Co.*, White's City, 1 ♂, 12.Jul.1966, coll. W.E. Ferguson (CISC); **Texas**, *Brewster Co.*: Big Bend National Park, Chisos Mts., The Basin, 5400–6000', 1 ♂, 9.May.1959, 3500–4000', 1 ♂, 24.May.1959, coll. W.R.M. Mason (EMUS), 1 paratype ♂, 8–14.Jul.1948, coll. H.E. Evans (NMNH), Panther Jct., 1 ♂, 31.Aug.1971, coll. E.E. Grissell and R.F. Denno; Chisos Mts., 1 paratype ♂, 10–12.Apr. 1908, coll. Mitchell and Cushman (NMNH). **MEXICO**: **Chihuahua**, 1 ♂, 13.Jul. 1964, coll. J.A. Chemsak (CISC); **Coahuila**, Serrino, Buena Vista, Sierra del Carmen, 6000', 2 ♂*, 18.Jul.1938, coll. R.H. Baker (UMSP, UAIC); **Durango**, Nombre de Dios, 1 paratype ♂, 4.Aug.1951, 1 paratype ♂, 5.Aug.1951, 1 paratype ♂, 6.Aug.1951, coll. H.E. Evans (NMNH), 1 ♂, 6.Aug.1951, coll. P.D. Hurd (EMUS).

Remarks.—Previously this species was known from the holotype and five paratypes. Although this species has a complete dorsal mandibular carina and lacks a clypeal tooth, the clypeal shape differs from *A. dorophora* and *A. snellingi*, **sp. nov.**, which also have this set of characters.

Acanthophotopsis falciformis Schuster

Acanthophotopsis falciformis falciformis Schuster, 1958. Ent. Amer. (n. s.) 37: 13 (in key), 108. male. Holotype: California, Palm Springs, fall.1932, coll. T. Zschokke (UMIC).

Acanthophotopsis falciformis furcisterna Schuster, 1958. Ent. Amer. (n. s.) 37: 14 (in key), 111. male. Holotype: Arizona, Tucson, 5.Oct.1935, coll. O. Bryant (UMIC). **NEW SYNONYM**.

Male diagnosis.—*Acanthophotopsis falciformis* is easily identified by the presence of a fourth mandibular tooth, which is found along the internal margin and projects posteriorly over the apex of the clypeus (Fig. 6). Other characters useful in identifying *A. falciformis* are: 1) the dorsal carina of the mandible extends from the base of the mandible to the innermost tooth; 2) the base of the clypeus is slightly raised, although neither carinate nor tuberculate and not horizontally produced; 3) the frons is coarsely punctate while the vertex is moderately punctate; 4) the length of the first flagellomere is 2× its width; 5) the head behind the eyes is strongly convergent (Fig. 12); 6) the length of the stigma is 0.8× the length of the marginal cell along the costa; and 7) the paramere in lateral view is equally broad throughout its length except for the apex, which narrows to an acute angle, and the paramere is as broad as the cuspis medially (Fig. 18).

Material examined.—**USA: Arizona**, *Apache Co.*: McNary, 1 ♂, 4.May.1963, coll. Bedall (UAIC); *Coconino Co.*: 2 ♂, 16.Aug.1940, 5 ♂, 23.Aug.1940, coll. F.W. Nunenmacher (UMSP); *Gila Co.*: Christmas, 3 mi SW nr Gila River, 1 ♂, 4.Jun.1962, coll. F. Werner (UAIC); Globe, 1 ♂, 8.Aug.1933, 1 ♂, 18.Aug.1936, coll. F.H. Parker (UMSP); La Paz Co.: Ehrenberg, 5 ♂, 22.Mar.1940 (UMSP); Graham Co.: Bonita

Creek, 3500', 1 ♂, 17.Aug.1976, coll. D.S. Chandler (UAIC); *Maricopa Co.*, Maricopa Mts., 1 ♂, 12.Apr.1947, coll. H.&M. Townes (AEIC); Phoenix, 17.May.1941 (UMSP); Mesa, 8 mi. NE, 1 ♂, 28.Apr.1964, coll. W.E. Ferguson (CASC); *Pima Co.*, Ajo, 2 ♂, 8.Apr.1947, coll. H.&M. Townes (AEIC); Arizona Sonora Desert Museum, 5 ♂, 9–16.Aug.1962, 4 ♂, 21–24.Aug.1962, coll. W.L. Nutting and S. Owen (UAIC); Ajo Mts., Alamo Canyon, 1 ♂, 24.Jul., coll. J.W. Green (CASC); Organ Pipe Nat. Mon., 2 ♂, 14.Apr.1955, coll. Butler and Werner (UAIC), 1 ♂, 17.Apr.1955, coll. J. Eden (UAIC), 3 ♂, 17.Aug.1955, coll. J. Eden (UAIC); Pusch Peak, W slope, Santa Catalina Mts., 2800', nr Hardy Rd and Hwy 80, 1 ♂, 17.May.1963, coll. C.E. Mickel (UMSP); Sabino Cyn., Santa Catalina Mts., 1 ♂, 22.Apr.1965, coll. J. Hessel and J. Burger (UAIC); Saguaro Nat. Mon., 1 ♂, 18.May.1961, coll. G.D. Butler (UAIC); Tucson, 1 ♂, 4.May.1963, 2 ♂, 6.May.1963, 1 ♂, 12.May.1963, 1 ♂, 8.May.1963, 1 ♂, 14.May.1963, coll. C.E. Mickel (UAIC), 10.Aug.1959, coll. K.W. Radford (UAIC), 1 ♂, 9.Aug.1928, coll. A.A. Nichol (UAIC), 16 ♂, 26.Aug.1939, coll. O. Bryant (UMSP); Tucson, N end Campbell Ave., Santa Catalina Foothills, 6 ♂, 5.Aug.1967, coll. M.S. Noller (UAIC); Tucson Mtn Park, 1 ♂, 14.Apr.1990, coll.W.E. Ferguson (CASC); *Santa Cruz Co*: Patagonia, 1 ♂, 21.Aug.1940, coll. F.W. Nunenmacher (UMSP); *Yuma Co.*: Tinajas, Atlas Mts., 1 ♂, 26.Aug.1930, coll. L.K. Gloyd (EMUS).**California**, Algodones Dunes, Niland-Glamis Rd., 7.4 km NW Glamis, 1 ♂, 3–30.May.2008, S. Heydon and K. Lorenzen (UCDC); *Imperial Co.*, Glamis, 3.5 mi NW, Algodones Dunes, 1 ♂, 13.Apr.1964, (UCRC); Glamis, 7 mi. E, 5 ♂, 11–12.Apr.1973, M.S. Wasbauer (CDFA); Pothole, 1 ♂, 9.Apr.1923, coll. E.P. VanDusee (CASC); *Riverside Co.*: Corn Spg., 5 mi. S Desert Center, 2 ♂, 24.Jun.2004, coll. K.A. Williams (KAWC); Deep Canyon, 5 ♂, 2.May.1963, coll. E.I. Schlinger (UCRC), 2 ♂, 3.May.1963, coll. E.I. Schlinger (UCRC), 3 ♂, 16.May.1963, coll. E.I. Schlinger (UCRC), 1 ♂, 30.May.1963, coll. E.I. Schlinger (UCRC), 2 ♂, 8.Oct.1963, coll. M.E. Irwin and E.I. Schlinger (UCRC),12 ♂*, 9.Oct.1963, coll. M.E. Irwin and E.I. Schlinger (UCRC, EMUS); McCoy Springs, 8.Apr.1963, coll. E.I. Schlinger and J.C. Hall (UCRC); Palm Desert, 1 ♂, 11.Apr.1950, coll. L.W. Quate (EMUS); Junction Horsethief Cr. and Deep Cr., 8 mi. N, 2960 ft, 3 ♂, 30.Jun.–1.Jul.1969, coll. A. Tabet (UCRC); Palm Cyn Dr. and Bogart Tr., 1 ♂, 23.May.2001, coll. D. Hawks (UCRC); PL Boyd Des. Res. Center, Deep Canyon, 1 ♂ (UCRC); PL Boyd Des. Res. Center, 2 ♂, 18.May. 1969, coll. M.E. Erwin (UCRC); PL Boyd Des. Res. Center, 2 ♂, 21–29.May. 1973, coll. A.B. Tabet (UCRC); PL Boyd Des. Res. Center, 2 ♂, 27.May.–1.Jun.1970, coll. S. Frommer and R. Worley (UCRC); PL Boyd Des. Res. Center, 2 ♂, 18.May. 1969, coll. M.E. Erwin (UCRC); PL Boyd Des. Res. Center, 1 ♂, 24.May.1969, coll. M.E. Erwin and S. Frommer (UCRC); PL Boyd Des. Res. Center, 3 ♂, 13–18.Jun.1969, coll. S. Frommer and B. Worley (UCRC); PL Boyd Des. Res. Center, 1 ♂, 15.Jun.1969, coll. S. Frommer and L. LaPré (UCRC); PL Boyd Des. Res. Center, 3 ♂, 18–19.Jun.1969, coll. S. Frommer and B. Worley (UCRC); PL Boyd Des. Res. Center, 4 ♂, 20–24.Jun.1969, coll. S. Frommer and B. Worley (UCRC); PL Boyd Des. Res. Center, 3 ♂, 2–3.Jul.1969, coll. S. Frommer and R.M. Worley (UCRC); *San Bernardino Co.*: Baker, 9 air mi. S, Zzyzx Sprs., 1 ♂, 22.Apr.1977, coll. Buegler (CISC), Needles, 1 ♂, 5.May.1939, coll. E.P. VanDuzee (CASC), Rice, 4 mi. S, 5 ♂, 3.Aug.1962, coll. W.E. Ferguson (CASC); Zyzzyx, Soda Springs, 1 ♂, 9.Aug.1986, coll. R.A. Read (EMUS). *San Diego Co.*, Borrego V, 1 ♂, 20.May1941, coll. E.C. Van Dyke (CASC); **Nevada**, *Clark Co.*, Logandale, 1 ♂, 5.Aug.1959. coll. F.D. Parker (NVDA); *Nye Co.* Mercury, 1 ♂, 21.Aug.1964 (BYUC); 5 ♂, 23.Aug.1964 (BYUC). **MEXICO**: **Sonora**, 1 ♂, 1–10.Sep.1953, coll. B. Malkin (CASC).

Paratypes of *A. f. furcisterna*: Arizona, Tucson, 1 ♂, 26.Aug.1939, coll. O. Bryant (NMNH).

Paratypes of *A. f. falciformis*: California, Palm Springs, 1 ♂, fall 1932, coll. T. Zschokke (NMNH). Arizona, Ehrenberg, 1 ♂, 27.Apr.1939, coll. F.H. Parker (NMNH).

Remarks.—Schuster (1958) separated *A. falciformis sensu stricto* from *A. f. furcisterna* based on the shape of the head posterior to the eyes, with the former having poorly developed temples and a strongly convergent vertex in contrast to *A. f. furcisterna*, which has well developed temples and a more rounded vertex. A review of preserved museum specimens has failed to yield a noticeable difference in the shape of

the head. Schuster also reported that the metasoma of *A. f. furcisterna* was darker than in *falciformis*. We found this not to be the case. Some specimens of *A. f. furcisterna* from Arizona lack castaneous or piceous pigmentation ventral to the felt line and some specimens of *A. f. falciformis* from Riverside Co., California, have castaneous and piceous pigmentation ventral to the felt line.

Schuster (1958) also reported a difference in the size of the eyes of these two subspecies, as measured by the relative proportions of the frons and the width of the head. The frons of *A. f. falciformis* (0.47–0.49) is narrower than *A. f. furcisterna* (0.53–0.55) due to the encroachment of the eyes (Schuster, 1958). Our measurements, however, show that the range of *A. f. falciformis* (0.46–0.49) overlaps with the range of *A. f. furcisterna* (0.46–0.52), although *A. f. furcisterna* has, on average, a broader frons. Schuster (1958) also reported that that the ocelli in *A. f. falciformis* were very large with the ocellocular distance (1.15–1.25) much shorter than that in *A. f. furcisterna* (1.4–1.7). As with the relative width of the frons, we found that *A. f. furcisterna* has, on average, a larger distance between the eyes and ocelli relative to the length of the ocelli (1.4–1.5) than does that of *A. f. falciformis* (1.2–1.5), but there is much overlap in the ranges of these two subspecies.

Schuster (1958) reported that the mesosternal processes of *A. f. furcisterna* were sickle-shaped and differed from that of *A. f. falciformis*. We found variation and overlap in the shape of the processes between the two subspecies. We compared the basal width of the mesosternal process to their length in *A. f. furcisterna* (0.65–1.0) and *A. f. falciformis* (0.75–1.0), and found that proportional size of the process is similar between the two.

Lastly, study of the genitalia uncovers no discernable differences between these two subspecies. These discrepancies are not unexpected given that Schuster only had four specimens each of *A. f. falciformis* and *A. f. furcisterna* with which to work. Because of the overlap in the various measurements discussed above and lack of discernable differences, we consider these two subspecies synonymous.

Acanthophotopsis snellingi Tanner & Pitts, New Species

Male diagnosis.—Acanthophotopsis snellingi is distinguishable from the other species of *Acanthophotopsis* by having the following combination of characters.) The mandibles are tridentate, and the dorsal carina of the mandible is complete to the innermost tooth and the apex of the mandible is vertical (Fig. 7). The basal margin of the clypeus lacks a carina and a central tubercle, is horizontally produced and covered in short, dense setae. The head behind the eyes is elongate, with the margins of the head just posterior to the eyes almost parallel for a distance equal to one half the length of the eye (Fig. 13). Other characters useful in identifying *A. snellingi* are: 1) the frons is moderately punctate while the vertex has small punctation; 2) the length of F1 is 1.5–2× its width; 3) the length of the stigma is 0.8× the length of the marginal cell along the costa; and 4) the paramere, in lateral view is equally broad throughout its length except for the apex, which narrows to an acute angle, and the paramere is 4× as broad as the cuspis medially (Fig. 19).

Description.—Setal pattern and coloration: Body covered in brachyplumose setae that are uniformly white, except pale golden on mesonotum; most dense along posterior margins of tergites. Weak fringe of sparse white brachyplumose to plumose setae present on apical fringes of metasoma. Head, mesosoma and metasoma reddish-brown, except ocellar triangle dark reddish-brown, clypeus light reddish-brown, and apex of metasoma becoming piceous. Wings hyaline basally, veins brown, and slightly infuscate apically. Coxae and trochanters concolorous with body. Antennae,

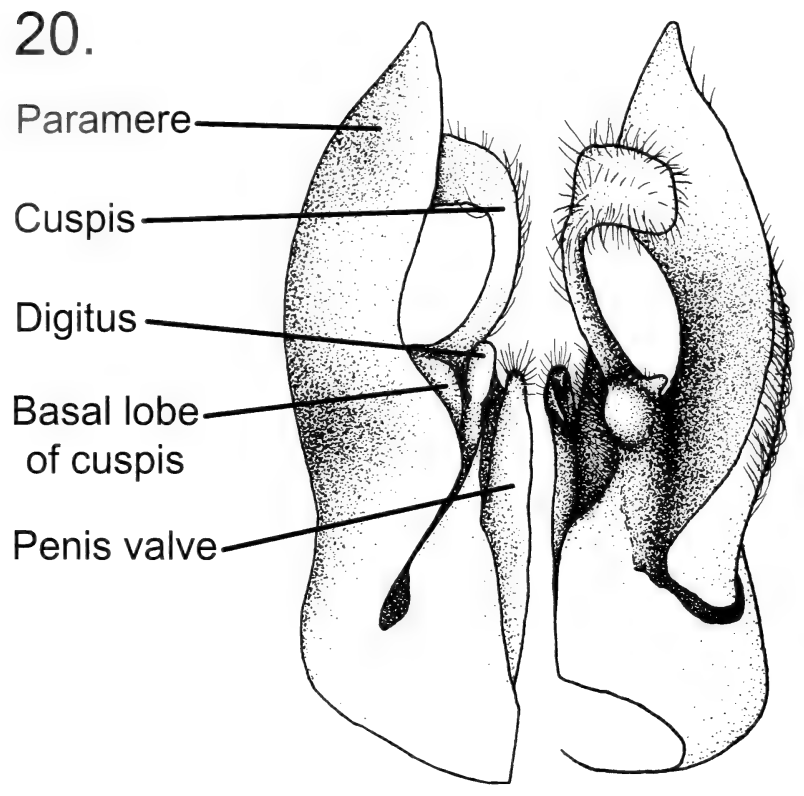


Fig. 20. Dorsal (left) and ventral (right) view of genitalia of *Acanthophotopsis snellingi*.

tibiae, femora, and tarsi noticeably darker than body, piceous, concolorous with apex of metasoma. Petiole concolorous with mesosoma.

Head.—Elongate posterior to eyes, lateral margin parallel for one half length of eye. Mandible tridentate; second tooth greatly reduced, attached to first tooth for almost entire length. Dorsal carina extending from mandible base to dorsal tooth. Clypeus without central tubercle or carinate basal margin; projecting anteriorly, horizontal. Interocular distance 3.5× eye width. Head moderately to coarsely punctate, glabrous between punctures. Ocellocular distance more than 2× diameter of lateral ocellus. Diameter of lateral ocellus as large as intraocellar distance. F1 3.3× as long as free length of pedicel. F2 3× as long as free length of pedicel. F3 2.7× as long as free length of pedicel.

Mesosoma.—Pronotum and mesopleuron continuously reticulate. Mesosternal process acutely triangular, directed posteriorly. Tegula triangular, glabrous apically. Propodeum continuously reticulate, with large areolets basally. Wings setose, setae dark brown. Middle tibia swollen, widest at apex. Stigma ~0.8× length of marginal cell along the costa.

Metasoma.—First segment petiolate with second. T1 coarsely punctate throughout. T2 and S2 weakly punctate. Remaining sclerites micropunctate. S2 lacking felt line. Pygidium glabrous, apical fringe present.

Genitalia.—Paramere stout, narrowing only at apex to acute angle (Figs 19, 20); setose only on external ventral margin (Figs 19, 20). Cuspis elongate, externally curved, spatulate apically (Figs 19, 20). Pit at base of cuspis large, extending across most of cuspis width, with long centrally

directed setae (Figs 19, 20). Digitus short, cylindrical, setose apically (Figs 19, 20).

Type Material.—HOLOTYPE: **Mexico**, *Zacatecas*, 9 mi S. of Fresnillo, 1 ♂, 18.Aug.1956, coll. D.D. Linsdale (CISC). PARATYPES: **Mexico**, *Zacatecas*, 9 mi S. of Fresnillo, 1 ♂, 20.Aug.1956, coll. D.D. Linsdale (CISC); *Chihuahua*, 32 mi S. Hidalgo de Parrel, 1 ♂, 21.Aug.1960, coll. P.H. Arnaud, Jr., E.S. Ross, D.C. Rentz (CASC).

Etymology.—Named in honor of Roy Snelling for his great contribution to Hymenoptera taxonomy.

Remarks.—*Acanthophotopsis snellingi* differs from *A. bequaertii* and *A. bifurca* by several characters. The mandible of *A. snellingi* has a complete dorsal carinae and the tip of the mandible is vertical. *Acanthophotopsis snellingi* lacks a posteromedial tubercle on the clypeus. Both *A. bequaertii* and *A. bifurca* have an incomplete dorsal carina on the mandible, the apex of the mandible is oblique, and they both possess a distinct posteromedial tubercle on the clypeus. Additionally, the length of the marginal cell along the costa relative to the stigma (approximately 1:1) in *A. bequaertii* is much larger than in *A. snellingi*. The legs and the metasoma are nearly black in *A. bequaertii*, whereas they are much lighter in *A. snellingi*. The quadridentate mandible of *A. falciformis* is not easily confused with that of *A. snellingi*.

Acanthophotopsis snellingi is most like *A. dorophora*. The antenna, however, of *A. dorophora* is much longer and more slender, than in *A. snellingi*. The second antennal segment is 3.75× longer than its width in *A. dorophora* and 2.5–3 times longer than its width in *A. snellingi*. The head behind the eyes is strongly convergent in *A. evansii*, while elongate *A. snellingi*. Lastly, the genitalia differ significantly (Figs 15, 19).

KEY TO THE SPECIES OF *ACANTHOPHOTOPSIS*

1 Mandible quadridentate: three apical teeth and fourth large tooth on internal margin whose apex forms an obtuse angle that overhangs the clypeus when mandible in repose; fourth tooth directed posteriorly and located ½ the distance from the base of the mandible (southern Utah, Nevada, Arizona, and California) ..... ***A. falciformis* Schuster**

\- Mandible tridentate 2

2(1) Dorsal carina on mandible not complete, ending before innermost apical tooth; base of clypeus with median longitudinal carina and central tubercle, apex of mandible oblique 3

\- Dorsal carina on mandible complete, extending from mandible base to innermost apical tooth, apex of mandible vertical (Figs 4, 5, and 7); base of clypeus without median longitudinal carina or central tubercle 4

3(2) Posterior margin of head elongate (Fig. 8); metasoma piceous; stigma as long as marginal cell along the costa; genitalia as in Fig. 14 (southeastern Arizona and Chihuahua and Durango, Mexico) ..... ***A. bequaertii* Schuster**

\- Posterior margin of head rounded and converging; metasoma reddish brown, at most apical segments darkened; stigma 0.75× the length of marginal cell along the costa; genitalia as in Fig. 15 (western Texas, Oklahoma and eastern New Mexico) ... ***A. bifurca* Schuster**

4(2) Head converging directly behind the eyes (Fig. 11); clypeus not plate-like, mostly vertical; genitalia as in Fig. 17; metasoma piceous (southeastern Arizona and Chihuahua and Coahuila, Mexico) ..... ***A. evansii* Schuster**

\- Head elongate posteriorly, lateral margins of head parallel for ½ the length of the eyes (Fig. 10, 13); clypeus plate-like, mostly horizontal; metasoma reddish brown, at most apical segments darkened 5

5(4) Paramere tapering towards apex (Fig. 16); marginal cell length ~1.05× length of stigma measured along costa; length of F1 greater than 2.5× its width (southwestern Arizona and southern California) ..... ***A. dorophora* Schuster**

- Paramere wide until just before apex (Fig. 19, 20); marginal cell length ~1.25× length of stigma measured along costa; length of F1 2.5× or less its width (Zacatecas, Mexico) ..... ***A. snellingi* Tanner & Pitts**

ACKNOWLEDGMENTS

We thank Kevin Williams (Utah State University, Logan, UT), Joe Wilson (Utah State University, Logan, UT), and Theresa Pitts-Singer (USDA-ARS Bee Biology and Systematics Laboratory, Logan, UT) for their thoughtful and helpful comments regarding this manuscript and Theresa Pitts-Singer (USDA-ARS Bee Biology and Systematics Laboratory, Logan, UT) for critically reviewing the manuscript. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah. Approved as journal paper no. 8066.

LITERATURE CITED

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Science Bulletin* 50: 483–648.

Ferguson, W. E. 1967. Male sphaeropthalmine mutillid wasps of the Nevada Test Site. *Brigham Young University Science Bulletin, Biology Series* 8: 1–26.

Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, D. C. 2735 pp.

Pitts, J. P. and J. V. McHugh. 2002. Revision of *Acrophotopsis* (Mutillidae: Sphaeropthalminae), with a new species from Baja California. *Journal of Hymenoptera Research* 11: 363–374.

Schuster, R. M. 1958. A revision of the sphaeropthalmine Mutillidae of America north of Mexico. II. *Entomologica Americana* 37: 1–130.

Wilson, J. S. and J. P. Pitts. 2008. Revision of velvet ant genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by using molecular and morphological data, with implications for desert biogeography. *Annals of the Entomological Society of America* 101: 514–524.

J. HYM. RES.
Vol. 18(2), 2009, pp. 205–211

Description of the Female of *Acrophotopsis* (Hymenoptera: Mutillidae) with Synonymy of *Sphaeropthalma dirce*

JAMES P. PITTS AND JOSEPH S. WILSON

Department of Biology, Utah State University, 5305 Old Main Hill, Logan, UT 84322-5305, USA; jpitts@biology.usu.edu

Abstract.—The female of *Acrophotopsis campylognatha* Schuster is described. *Sphaeropthalma dirce* (Fox), known from females only, is transferred to *Acrophotopsis* and is the **senior synonym** of *A. eurygnatha* Schuster. This represents the first description of females for *Acrophotopsis*. Most importantly, the females of *Acrophotopsis* can be diagnosed by the following unique combination of characters: having a distinct basal tooth on ventral margin of mandible and a tooth-like projection at the anterior termination of the dorsal mandibular carina; having the mesosoma and second metasomal tergite moderately punctate to reticulately sculptured and having rasp-like tubercles situated between the reticulations that are more apparent anteriorly; having the first metasomal segment petiolate with the second; having the pygidium laterally defined by carinae with granulate sculpturing; and having the propodeum and fringes of tergites two through four with distinct white plumose setae.

Key words.—velvet ant, Sphaeropthalminae, *Dilophotopsis*, ITS1 and ITS2

Acrophotopsis Schuster (Hymenoptera: Mutillidae) is an easily recognized genus of nocturnal mutillid possessing deeply excised mandibles, a flattened hypopygidium with lateral, basal carinae, and genitalic parameres that overlap *in situ*, while lacking mesosternal processes. The genus currently contains four species recently revised by Pitts and McHugh (2002). All species of *Acrophotopsis* are found in the southwestern U.S. and Mexico, and are known only from males (Manley and Pitts 2002). Although females of *Acrophotopsis* are unknown, they are presumed to be active at night similar to males. Nothing more is known about the biology of *Acrophotopsis*.

R.M. Schuster (1958) described the genus *Acrophotopsis* based on males of two species of previously undescribed nocturnal Sphaeropthalmini from the Nearctic region, *A. campylognatha* Schuster and *A. eurygnatha* Schuster. These two species are sympatric in the Mojave Desert. *Acrophotopsis campylognatha* occurs in Baja California and in the western Sonoran and Mojave Deserts of Southern California, while *A. eurygnatha* occurs in eastern Sonoran Desert of Arizona and Mexico, and into the Mojave Desert as far west as Nevada (Ferguson 1967). A third species, *A. bergi* Casal, was added to the genus later and occurs in central Mexico in the states of Jalisco, Morelos, and Puebla, Mexico (Casal 1967). The last species to be added to the genus was *A. mickeli* Pitts and McHugh, described from Baja California Sur (Pitts and McHugh 2002).

The genus is known from a single sex, in part, due to the extreme sexual dimorphism that occurs in mutillids (Brothers 1995). Nocturnal velvet ant males are easily collected in light traps, while females are rarely collected. Sex associations are further complicated by great morphological similarity among species. This makes associating sexes nearly impossible based on examination of museum specimens and

sex associations made by catching pairs *in copula* are rare. More advanced molecular techniques, however, can be used to make sex associations using species-specific genetic loci (Pilgrim and Pitts 2006; Pitts *et al.* 2007; Pilgrim *et al.* 2008).

The purpose of this study is to associate the females with the two species of *Acrophotopsis* found in the United States, *A. campylognatha* and *A. eurygnatha*.

MATERIALS AND TERMINOLOGY

Trapping methods.—Field studies were conducted throughout the Southwestern U.S. during the summers of 2005–2008 to collect fresh specimens of both sexes of nocturnal velvet ants to attempt associating the sexes using molecular techniques. Male and female nocturnal mutillids were collected at 60 field sites across the Southwestern U.S.

Specimens were collected using black light and fluorescent lantern traps, and by hand. Specimens collected with light traps were captured in soapy water and transferred into 95% ethanol, while all hand-collected specimens were placed directly into 95% ethanol.

Molecular methods.—The two internal transcribed spacers (ITS1 and ITS2) were sequenced for representatives of each available species and sex, sequences were aligned, and females were associated with males based on identical or nearly identical DNA sequences for those loci (i.e., very small genetic distances). The methods proposed by Pilgrim and Pitts (2006) were followed for performing sex associations. ITS1 and ITS2 were sequenced for at least one female of each morphospecies and several male specimens of each described species. PCR was used to amplify the ITS1 and ITS2 regions of the nuclear genome using the molecular protocols described in Pilgrim and Pitts (2006). DNA samples were sequenced in both directions and combined using Sequencher 4.0 (Gene Code Corp., Ann Arbor, MI). DNA sequences were aligned using Clustal W (Thompson, *et al.* 1994) and intraspecfic and interspecific genetic distances were calculated from these alignments. DNA sequences were deposited in GenBank (Accession Nos. GQ223230-GQ223237).

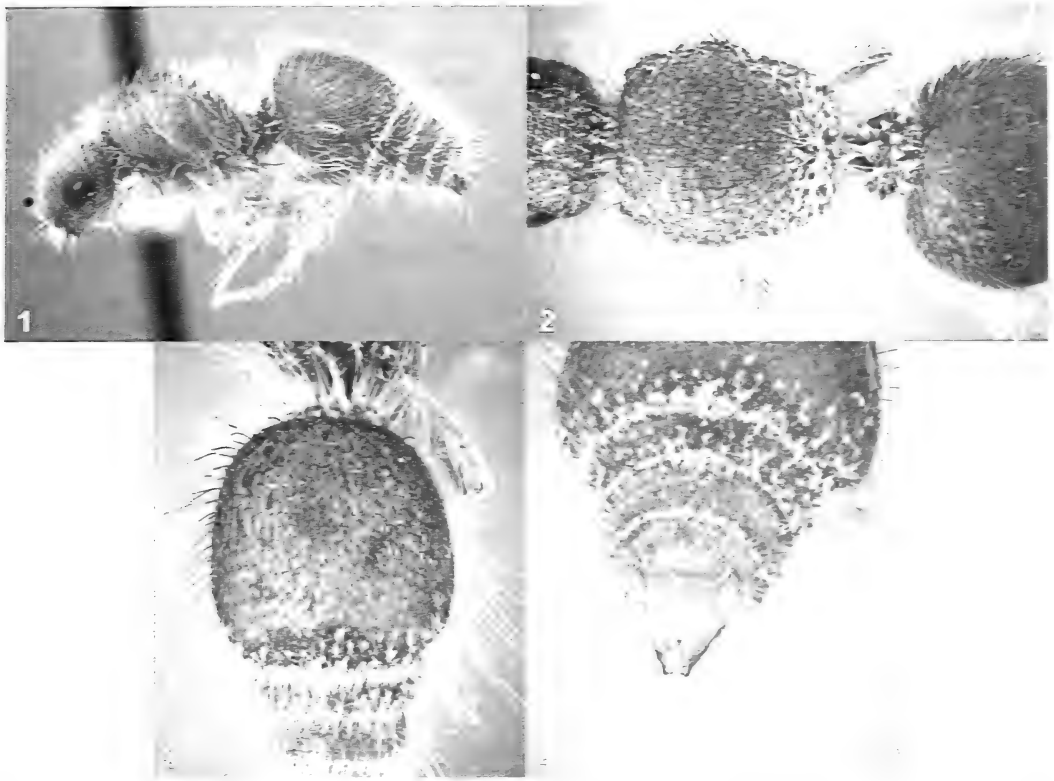
Taxonomic methods.—The following acronyms are for institutions or collections housing the material discussed in the current study: Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A. (ANSP); Department of Entomology, California Academy of Sciences, San Francisco, California (CASC); and Entomological Museum, Department of Biology, Utah State University, Logan, Utah, U.S.A. (EMUS).

We adopt the following notation after Ferguson (1967) for punctures in the order of decreasing coarseness: reticulate, coarse, moderate, small, fine and micropunctate. Micropunctate refers to punctures that are extremely shallow and do not have vertical walls or sharp margins. Small refers to punctures that do have slight vertical walls and are separated by at least 5× their diameter. We use the term "simple setae" for setae that are smooth and do not have barbed surfaces. "Brachyplumose setae" refers to setae with barbs that are less than, or equal to, the diameter of the shaft at the attachment of the barb. The term "plumose setae" is used for setae that have longer barbs. The term "tibial spurs" is used instead of "calcaria." The term "paramere" is used instead of "gonoforceps" to remain consistent with previous mutillid literature. The acronyms T2, T3, etc., denote the second, third, etc., metasomal tergites, respectively. Similarly, S2, S3, etc., signifies the second, third, etc., metasomal sternites, respectively.

Acrophotopsis Schuster

Acrophotopsis Schuster 1958. Ent. Amer. (n. s.) 37: 4 (in key), 61, male. Type species: *Acrophotopsis eurygnathus* Schuster, orig. desig.

Diagnosis of females.—The females of *Acrophotopsis* can be diagnosed by the



Figs 1–4. Female of *Acrophotopsis dirce*. 1. lateral view. 2. Dorsal view of mesosoma. 3. Dorsal view of the second metasomal tergite. 4. Dorsal view of the pygidium.

following unique combination of characters: they are nocturnal with reddish brown to brown integument; the compound eyes are only slightly ovate (Fig. 1); the mandible has a distinct basal tooth on ventral margin and a tooth-like projection at the anterior termination of the dorsal carina; the mesosoma is longer than broad and only slightly wider at the mesonotal spiracle than elsewhere (Fig. 2); the first metasomal segment is petiolate with the second (Figs 1 and 2); the mesosoma and second metasomal tergite are moderately punctate to reticulately sculptured and have rasp-like tubercles situated between the reticulations with the tubercles being more apparent anteriorly than posteriorly (Figs 2 and 3); the punctures, at least on the anterior half of the second tergite, have lateral margins that extend posteriorly appearing as a multitude of longitudinal ridges (Fig. 3); the pygidium is granulate and defined laterally by carinae (Fig. 4); and the propodeum and fringes of tergites two through four consists of distinct white plumose setae (Figs 2 and 3).

Acrophotopsis campylognatha Schuster

Acrophotopsis campylognathus Schuster 1958. Ent. Amer. (n. s.) 37: 11 (in key), 69. male. Holotype: MEXICO, Baja California, Arroyo Rosarito, 29.III.1935, coll. C.M. Brown (CASC).

Diagnosis of female.—The female of *A. campylognatha* can be separated from that of *A. dirce* by the mesosoma and second metasomal tergite being reticulately sculptured and the setae on the dorsum of the mesosoma and centrally on the second tergite being whitish and only slightly tinged reddish-brown.

Description of female.—**Coloration and Setal Pattern:** Body reddish-brown to brown. Mandibular apices black. Flagellum and legs yellow to dark yellow. Setae sparse in general, not concealing sculpture. Head, pleurae, and vertical face of propodeum with decumbent and erect white brachyplumose setae. Dorsum of mesosoma with decumbent and erect brachyplumose setae; setae white, but slightly tinged reddish-brown. Propodeal dorsum and vertical face with distinct, sparsely-spaced, white plumose setae. T1 covered with both decumbent white plumose setae and erect white brachyplumose setae. T2 with erect white brachyplumose setae, tinged light brown centrally; sparse short white plumose setae present on posterior third. T2–4 and S2–S5 with fringe of white plumose setae; fringe becoming sparser on more apical tergites. Fringe of T5 medially with light golden brachyplumose setae, laterally with white plumose setae. Legs with white brachyplumose setae.

Head.—Head rounded posteriorly, not as wide as mesosoma, densely punctate. Eye slightly ovate, distance from posterior mandibular articulation ~2.5× length of pedicel. Clypeus protruding anteriorly, posteromedially produced into low triangular swelling with central tubercle. Antennal scrobe without dorsal carina. Antennal tubercle glabrous, except with carinate apical margin. Flagellomere I ~1.2× length of pedicel. Flagellomeres II–III ~1.0–1.2× length of pedicel. Flagellomeres I–III subequal in length. Flagellomeres II–X produced apically on ventral side; appearing crenulate. Mandible bidentate apically. Dorsal mandibular carina with tooth-like projection at anterior termination of carina. Ventral mandibular margin with large basal tooth; lacking excision apical to ventral tooth. Genal carina absent.

Mesosoma.—Mesosoma wider anteriorly than posteriorly, longer than broad. Mesosoma reticulate on dorsum, some reticulations with margin appearing tuberculate; punctures becoming larger and without tubercles posteriorly. Propleuron punctate anteriorly. Humeral angle dentate. Epaulet prominent. Scutellar scale absent. Mesopleuron punctate medially. Mesosternum with low transverse tubercle present medially just anterior to mesocoxa. Metasternum tridentate, median tooth ~4× as long as lateral teeth. Extreme ventral region of lateral margin of propodeum punctate. Mid- and hind-tibiae with two rows of spines on outer margin and each with pair of tibial spurs.

Metasoma.—Segment 1 distinctly petiolate with segment 2. T1 with small sparse punctures. T2 with large reticulations on anterior half with tubercles situated between reticulations, becoming more sparsely punctate posteriorly. Reticulations and punctures with lateral margins extending posteriorly forming longitudinal carinules, even in sparsely punctate region. T2 with felt line; length 0.20× length of tergite. T3–T5 shagreened. T6 with distinct pygidial area defined laterally by weak carinae; surface granulate. S2 with slight anteromedian tumid region. S2–S5 with punctation similar to tergites.

Length: ~5.6 mm.

Dna voucher specimen data.—**California**, *San Bernardino Co.*: 5 mi S Barstow, 1 ♀, 30.May.2005, E.E. & K.A. Williams, KW14; 1 ♂, 30.May.2005, E.E. & K.A. Williams, JP324 (EMUS).

Distribution.—*Acrophotopsis campylognatha* is present in the southern regions of the Mojave Desert of California and into the Sonoran Desert of Baja California.

Remarks.—This sex association is based on molecular data. A total of 1,432 base pairs (504 bp for ITS1 and 928 bp for ITS2) was used to associate the male and female of this species. Both the ITS1 and ITS2 loci are identical between the male and female and this distance is much smaller than the interspecific genetic distance between *A. campylognatha* and *A. dirce* (8% for ITS1; 11% for ITS2).

Acrophotopsis dirce (Fox)

Mutilla dirce Fox, 1899. Amer. Ent. Soc., Trans. 25: 257, female. Holotype: Arizona, Tucson, coll. Wickham, type no. 4651 (ANSP).

Acrophotopsis eurygnathus Schuster 1958. Ent. Amer. (n. s.) 37: 11 (in key), 65, male. Holotype: USA, Arizona, Gila Co., Globe, 8.VII.1949, coll. Werner & Nutting (CASC). **NEW SYNONYM.**

Diagnosis of female.—The female of *A. dirce* can be separated from that of *A. campylognatha* by the mesosoma and second metasomal tergite being only densely punctate (Fig. 3) and the setae on the dorsum of the mesosoma and centrally on the second tergite being distinctly reddish-brown.

Redescription of female.—**Coloration and Setal Pattern:** Body reddish-brown to brown. Mandibular apices black. Flagellum, scape and legs yellow to dark yellow. Setae sparse in general, not concealing sculpture (Figs 1 and 2). Head, pleurae, and vertical face of propodeum with decumbent and erect white brachyplumose setae (Fig. 2). Dorsum of mesosoma with decumbent and erect brachyplumose setae (Fig. 2); setae reddish-brown. Propodeal dorsum and vertical face with distinct sparsely spaced white plumose setae (Fig. 2). T1 covered with both decumbent white plumose setae and erect white brachyplumose setae (Fig. 2). T2 with erect white brachyplumose setae, reddish brown centrally; sparse short white plumose setae present on posterior third (Fig. 3). T2–4 (Figs 3 and 4) and S2–S5 with fringe of white plumose setae; fringe becoming more sparse on apical tergites. Fringe of T5 medially with light golden brachyplumose setae, laterally with white plumose setae. Legs with white brachyplumose setae.

Head.—Head rounded posteriorly, not as wide as mesosoma, densely punctate. Eye slightly ovate, distance from posterior mandibular articulation ~2.5× length of pedicel (Fig. 1). Clypeus protruding anteriorly, posteromedially produced into low triangular swelling with central tubercle. Antennal scrobe without dorsal carina. Antennal tubercle glabrous, except with carinate apical margin. Flagellomere I ~1.2× length of pedicel. Flagellomeres II–III ~1.2–1.3× length of pedicel. Flagellomeres I–III subequal in length. Flagellomeres II–X produced apically on ventral side; appearing crenulate. Mandible bidentate apically. Dorsal mandibular carina with tooth-like projection at anterior termination of carina. Ventral mandibular margin with large basal tooth; lacking excision apical to ventral tooth. Genal carina absent.

Mesosoma.—Mesosoma wider anteriorly than posteriorly, longer than broad (Fig. 2). Mesosoma confluently punctate on dorsum, some reticulations with margin appearing tuberculate; punctures becoming somewhat reticulate posteriorly, but without tubercles (Fig. 2). Propleuron anteriorly, mesopleuron medially, and extreme ventral region of lateral margin of propodeum punctate. Humeral angle dentate. Epaulet prominent. Scutellar scale absent. Mesosternum with low transverse tubercle present medially just anterior to mesocoxa. Metasternum tridentate, median tooth ~4× as long as lateral teeth. Mid- and hind-tibiae with two rows of spines on outer margin and each with pair of tibial spurs.

Metasoma.—Segment 1 distinctly petiolate with segment 2 (Fig. 1 and 2). T1 with small sparse punctures. T2 confluently punctate on anterior half with tubercles situated between reticulations, becoming sparsely punctate posteriorly (Fig. 3). Reticulations and punctures with lateral margins extending posteriorly forming longitudinal carinules, but not in sparsely punctate region. T2 with felt line; length 0.20× length of tergite. T3–T5 shagreened. T6 with distinct pygidial area defined laterally by weak carinae; surface granulate (Fig. 4). S2 with slight anteromedian tumid region. S2–S5 with punctation similar to tergites.

Length: ~7 mm.

Dna voucher specimen data.—**USA: Arizona**, *Santa Cruz Co.*: 5 km W Peña Blanca Lake at Rt 39; Atascosa Mts, 1 ♂, 3/7.May.2004, M.E. Irwin & F.D. Parker, JP84 (EMUS). **MEXICO: Sonora**, Rancho Palo Injerto, 20 km E Alamos: 1 ♂, JP680, Jun.2006, 1 ♂, 28/31.Jun.2007, JP686 M.E. Irwin & F.D. Parker (EMUS).

Material examined.—USA: **Arizona**, *Cochise Co.*: Leslie Canyon NWR, 1 ♀, 19.May.2000, W.R. Radke (EMUS); **Nevada**, *Nye Co.*: Mercury: 1 ♀, 12.Aug.1964, 1 ♀, 14.Aug.1964, 1 ♀, 13.Jun.1961 (BYUC); **New Mexico**, *Hidalgo Co.*: Stone Cabin, U-Ranch, 1 ♀, 15.Jul.1977, Muma & Packard (EMUS); *Socorro Co.*: Sevilleta NWR, 1 ♀, 26.Oct.1992 (EMUS).

Distribution.—*Acrophotopsis dirce* has been collected from the Mojave Desert of Nevada to the Sonoran Desert of Arizona and Mexico.

Remarks.—The sex association is based on the similarities of the female described here with the female associated with *A. campylognatha* and the known distribution of *A. eurygnatha*. The type specimen of *A. dirce* was collected in Tucson, Arizona, and does not differ from other specimens from farther east in Arizona and New Mexico. These specimens are found in the same areas as the *A. eurygnatha* male. While no females were available for molecular comparisons, the available intraspecific genetic distances between males was low (0.0–0.3% for ITS1).

DISCUSSION

These are the first females to be associated with this genus. Only three nocturnal genera in the Nearctic region, *Acanthophotopsis* Schuster, *Laminatilla* Pitts, and *Schusterphotopsis* Pitts remain known only from a single sex. Ferguson supposedly associated a female with *A. eurygnatha* during his study at the Nevada Test Site, which was cryptically listed in Allred (1973), but he apparently never described the female and we have been unable to find the specimens referred to in Allred's manuscript.

The females of *Acrophotopsis* are easy to recognize as belonging to the genus. Disregarding setal color, they will key out to *Dilophotopsis* Schuster in Manley and Pitts (2002), from which they can be immediately separated by the presence of the anterior tooth at the termination of the dorsal mandibular carina and the presence of scattered tubercles on the metasoma. There are other nocturnal females that have a subset of these characters that could be confused with *Acrophotopsis*, but all lack the scattered tubercles on the mesosoma and metasoma. Specifically, *Sphaeropthalma laodamia* (Fox) and *Stethophotopsis maculata* Pitts both have longitudinal carinae on the second tergite, but *Sp. laodamia* has a distinct dorsal carina on the scrobe, while *St. maculata* lacks this carina (Pitts and Manley 2002). Additionally, *Sp. laodamia* and *St. maculata* have neither a large ventral tooth, nor a dorsal tooth on the mandible. They also lack tubercles on the mesosoma and second tergite, and lack a laterally defined pygidium. The male of *Sp. laodamia* is unknown, but this species seems to be placed in the correct genus. Lastly, *Sp. unicolor* (Cresson) has a dorsal tubercle on mandible, but lacks a large ventral tooth and has a sessile attachment metasomal segment 1 to metasomal segment 2.

It is rather difficult to differentiate the species of *Acrophotopsis* based on females. This is not surprising given the difficulty of separating the females of other related taxa (e.g. Pitts et al. 2004; Pitts 2006). The two *Acrophotopsis* species apparently differ only in the coarseness of the sculpturing on the dorsum of the mesosoma and second tergite of the metasoma, as well as in subtle setal coloration differences in these same areas. The two species do not overlap greatly in range, and, therefore, locality data can also be a good indicator for identifying the females. The males of these species, on the other hand, are not difficult to distinguish and differ in several characters, such as shape of the cuspis of the genitalia (Pitts and McHugh 2002).

Wilson and Pitts (2008) recently concurred along with Pitts and McHugh (2002) and Pitts (2003) in suggesting that *Dilophotopsis* and *Schusterphotopsis* Pitts are closely related to *Acrophotopsis*. The females of *D. concolor* and *D. stenognatha* (Cresson) have been described (Mickel 1963; Pitts *et al.* 2007) and can be compared to the females

of *Acrophotopsis*. The female of *Dilophotopsis paron* (Cameron) remains unknown. The females of these two genera are morphologically quite similar and share several notable characteristics, such as a large basal tooth on the ventral margin of the mandible, as well as the dorsal carina of the mandible terminating in a semi-erect tooth and the granulate sculpturing of the pygidium. The females of *Dilophotopsis*, however, have a longer first flagellomere, have more distinct plumose setal fringes on the metasoma, but lack the erect tubercles on the dorsum of the second metasomal tergite. In some cases the dorsum of the mesosoma of *D. concolor* has indistinct tubercles, but never to the degree of *Acrophotopsis*. Although not all of the females of *Dilophotopsis* are known, the similarities of the females of these taxa further strengthens the assertion that *Dilophotopsis* and *Acrophotopsis* are sister groups. In addition, the females of these genera share many characteristics with females of the *Sphaeropthalma orestes* species-group, more so than with other *Sphaeropthalma* females, and suggesting that *Sphaeropthalma* may be a paraphyletic assemblage.

ACKNOWLEDGMENTS

We would first like to thank Carol von Dohlen at Utah State University for the use of laboratory space and equipment. We also thank Erik Pilgrim and Carrie Drake for help with DNA extraction, PCR, and DNA sequencing and Sarah Clark for label data entry and voucher specimen curation. We thank David Tanner (Utah State University, Logan, UT) and Kevin Williams (Utah State University, Logan, UT) for critically reviewing drafts of this paper. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, UT and was approved as journal paper no. 8063.

LITERATURE CITED

Allred, D. M. 1973. Additional records of mutillid wasps from the Nevada Test Site. *Great Basin Naturalist* 33: 156–162.

Brothers, D. J. 1995. Mutillidae. Pp. 541–548 *in* Hanson, P. E. and I. D. Gauld, eds. *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford.

Casal, O. H. 1967. Comentarios sobre *Acrophotopsis* Schuster, con la descripción de una nueva especies de México (Hymenoptera: Mutillidae). *Physis* 74: 1–4.

Ferguson, W. E. 1967. Male sphaeropthalmine mutillid wasps of the Nevada Test Site. *Brigham Young University Science Bulletin, Biological Series* 8: 1–26.

Manley, D. G. and J. P. Pitts. 2002. Key to the genera and subgenera of Mutillidae of America North of Mexico with description of new genus. *Journal of Hymenoptera Research* 11: 72–101.

Mickel, C. E. 1963. Description of the female of *Dilophotopsis stenognatha* Schuster (Hymenoptera: Mutillidae). *Pan-Pacific Entomologist* 39: 183–184.

Pilgrim, E. M. and J. P. Pitts. 2006. A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of Kansas Entomological Society* 79: 222–230.

Pitts, J. P. 2003. *Schusterphotopsis*, a new genus of Sphaeropthalmini (Mutillidae: Sphaeropthalminae) from California, with notes on the closely related genera *Acrophotopsis* Schuster and *Dilophotopsis* Schuster clade. *Zootaxa* 333: 1–7.

———. 2006. Review of the *Sphaeropthalma imperialis* species-group (Hymenoptera: Mutillidae), with descriptions of females and taxonomic notes. *Zootaxa* 1248: 1–20.

——— and J. V. McHugh. 2002. Revision of *Acrophotopsis* (Mutillidae: Sphaeropthalminae), with a new species from Baja California. *Journal of Hymenoptera Research* 11: 363–374.

——— and D. G. Manley. 2002. Description of the females of *Stethophotopsis* Pitts and *Photopsioides* Schuster (Hymenoptera: Mutillidae). *Proceedings of the Entomological Society of Washington* 104: 672–679.

———, T. J. Boud, and E. M. Pilgrim. 2007. Molecular sex association of three species of nocturnal velvet ant (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 80: 136–145.

———, F. D. Parker, and T. L. Pitts-Singer. 2004. A review of the *Sphaeropthalma uro* species-group (Hymenoptera: Mutillidae), with taxonomic changes. *Journal of the Kansas Entomological Society* 77: 223–234.

Schuster, R. M. 1958. A revision of the sphaeropthalmine Mutillidae of America north of Mexico. II. *Entomologica Americana* 37: 1–130.

Thompson, J. D., D. G. Higgins, and T. J. Gibson. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673–4680.

Wilson, J. S. and J. P. Pitts. 2008. Revision of velvet ant genus *Dilophotopsis* (Hymenoptera: Mutillidae) by using molecular and morphological data with implications to desert biogeography. *Annals of the Entomological Society of America* 101: 514–524.

J. HYM. RES.
Vol. 18(2), 2009, pp. 212–226

Species Boundaries of *Sphaeropthalma unicolor* (Hymenoptera: Mutillidae): Is Color Useful for Differentiating Species?

JOSEPH S. WILSON AND JAMES P. PITTS

Department of Biology, Utah State University, 5305 Old Main Hill, Logan, UT 84322-5305, USA; jwilson@biology.usu.edu

Abstract.—Taxonomists often use differences in color to diagnose species. This is especially true for velvet ant species (Hymenoptera: Mutillidae), which often are recognized by differences in integumental and setal coloration. Recent molecular analyses have shown that color characteristics are not always useful in distinguishing among mutillid species. Morphological and molecular data are used here to investigate the different color forms of one of the most variable nocturnal velvet ants, the widespread species *Sphaeropthalma unicolor* (Cresson). This analysis also includes some less variable, but closely related species from the *S. unicolor* species-group (Group *rustica sensu* Schuster 1958). Differences were found in genitalic morphology, as well as in the ITS1 and ITS2 rDNA sequences between two distinct color forms. The species boundaries of *S. unicolor* and *S. mendica* (Blake), **new status,** are defined. We report that *Mutilla aspasia* (Blake) and *Photopsis nebulosus* (Blake) are **junior synonyms** of *S. mendica*. Also, the female of *S. angulifera* Schuster is described.

Key words.—Sphaeropthalminae, velvet ant, color characters, species boundaries

Color characters have often been employed by insect taxonomists to differentiate between species. Sometimes, however, using color alone is insufficient to distinguish species due to mimicry complexes (e.g., *Heliconius* butterflies; Sheppard et al. 1985) or highly variable species (e.g., *Dasymutilla quadriguttata* (Say); Pilgrim et al. 2009). Wasps in the family Mutillidae have often been identified largely using differences in setal coloration or integumental pigmentation (Mickel 1924, 1928, 1935, 1936, 1939, 1941, 1943, 1960; Manley 2003; Manley and Pitts 2007; Manley and Williams 2005; Williams and Manley 2006; Pilgrim et al. 2008; Williams and Pitts 2008a). The increased use of molecular tools, particularly the two internal transcribed spacer regions (ITS1 and ITS2), has enabled researchers to determine species boundaries when morphology is ambiguous (Pilgrim and Pitts 2006; Wilson and Pitts 2008; Pitts et al. 2009).

Recent work on the diurnal genera *Dasymutilla* Ashmead and *Pseudomethoca* Ashmead suggests that increased caution needs to be used when determining whether or not an alternate color form is, indeed, a distinct species. Pilgrim et al. (2008) showed that two species of *Dasymutilla* had been incorrectly described as separate species based, in large part, on the differences in their coloration. Also, Williams and Pitts (2008b) showed that three species of *Pseudomethoca* were improperly classified as one species, largely because they all shared a similar color pattern.

Color has also been used to differentiate between species and subspecies of nocturnal mutillids (e.g. Schuster 1958). Ferguson (1962), however, suggested that pigmentation in sphaeropthalmine mutillids was affected by the temperature and humidity during development. Molecular methods were used to show that the subspecies of the nocturnal mutillid *Dilophotopsis concolor* (Cresson), which were defined principally based on differences in pigmentation, were invalid (Wilson and Pitts 2008).

It is probable, however, that differences in color do sometimes reflect species-level differences among members of the family Mutillidae. For example, *Dasymutilla asteria* Mickel and *D. sicheliana* (Saussure) are molecularly distinct, yet are nearly identical structurally. These species, however, can be recognized based on differences in setal coloration. Also, the nocturnal species in the *S. imperialis* species-group, such as *Sphaeropthalma marvesia* (Blake) and *S. megagnathos* Schuster, can be identified by differences in their color patterns (Pitts 2006).

Sphaeropthalma unicolor (Cresson) is a common, wide-ranging nocturnal mutillid. The specific epithet given to this wasp is unfortunate, because this species is polymorphic in both setal coloration and cuticular pigmentation. Males exhibit three distinct color forms: some specimens have a reddish-black integument with yellowish wings; others have a reddish-brown integument with clear wings and white pubescence on the metasoma; and, lastly, there are others with yellowish-brown integument, clear wings and orange pubescence on the metasoma. Females also are found in two main color forms: some are covered with setae ranging from red to yellow, while the others have distinct white setae on the fringes of the metasomal segments. The extreme variability in the coloration of this wasp has led to numerous synonyms being described, largely based on differences in coloration. Ferguson (1967) synonymized nine names with *S. unicolor* based on the study of over 1,000 specimens. Interestingly, he insinuated that the difference in coloration of the forms is linked to elevation, stating that the Melanistic-color form was only found in higher elevations across the Great Basin and Mojave Deserts, while the Reddish-brown color form was present only in the lower elevations (Ferguson 1967). The allopatry observed by Ferguson (1967) in the two distinct color forms suggests elevation could be a barrier to gene flow, and that these two forms may represent distinct species.

This paper reports on molecular and morphological examinations that test the species boundaries of *S. unicolor*. The species-specific loci 1st and 2nd internal transcribed spacer regions (ITS1 and ITS2) and morphology are used to determine if the different color forms of *S. unicolor* represent distinct species by comparing genetic distances between color forms, and related species.

In the course of this study, the female of a closely related species, *S. angulifera* Schuster, was found. We described the female here and compared it to that of *S. unicolor*.

MATERIALS AND METHODS

Sampling

Specimens were collected from sites across western North America from 2002 to 2007 using black light traps, fluorescent lantern traps, and by hand. All specimens were placed directly into 95% ethanol and those used for molecular examination have been labeled as voucher specimens and deposited in the Department of Biology Insect Collection, Utah State University, Logan, UT (EMUS). All holotypes were examined and compared to molecular voucher specimens. An attempt was made to sample *S. unicolor* from all parts of its range and from each of its different color forms.

Three outgroups, *Sphaeropthalma angulifera*, *S. rinalea* Schuster and *S. triangularis* (Blake), were included in the analysis, because they are closely related to *S. unicolor* (Schuster 1958; Pitts unpub. data). Although Schuster (1958) included four other species in the *S. unicolor* species-group, we did not include *S. pluto* (Fox) or *S. juxta* (Blake) because they are so genetically different from the other members of the species-group that they obviously do not belong in the group. We were also

unable to include *S. tetricuspis* Schuster and *S. subtriangularis* Schuster, because they are found in Baja California and no fresh specimens were available from this area for molecular analysis.

Morphological analysis

All specimens were examined with a Wild M-5 stereo microscope and all measurements were made with an ocular micrometer. Eye size of females was determined by measuring the maximum longitudinal length of the eye compared to the length from the posterior margin of the eye to the vertex of the head. Eye length is reported as a ratio of the eye length to the eye-to-vertex length. Specimens were borrowed from or deposited into the following collections:

ANSP Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

BYUC Entomology Section, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA.

CISC Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, California, USA.

CSCA California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California, USA.

EMUS Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.

LACM Insect Collection, Los Angeles County Museum of Natural History, Los Angeles, California, USA.

NVDA Nevada State Department of Agriculture, Reno, Nevada, USA.

PMNH Peabody Museum of Natural History, Yale University, New Haven Connecticut, USA.

UCDC The Bohart Museum of Entomology, University of California, Davis, California, USA.

UCRC UCR Entomological Teaching and Research Collection, University of California, Riverside, California, USA.

UMSP University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

USNM United States National Entomological Collection, Department of Entomology, U.S. National Museum of Natural History, Washington D.C., USA.

Molecular analysis

DNA was extracted, amplified, and sequenced from individuals from each of the three color forms of *S. unicolor*, as well as some related species. DNA extraction and amplification of the two rDNA internal transcribed spacer regions (ITS1 and ITS2) followed the protocols outlined by Pilgrim and Pitts (2006). Sequences were analyzed with an ABI Prism 377, 3100, or 3730 Genetic Analyzer. All PCR products were sequenced in both directions and were combined in Sequencher 4.1 (Gene Code Corp., Ann Arbor, MI). Pair-wise percent genetic distances between subspecies were calculated by determining the number of differences (point mutations and insertions or deletions) and dividing by the number of base pairs of the longer of the two sequences. Gel electrophoresis of each gene yielded a single band for each individual wasp and the resulting DNA was sequenced cleanly suggesting no gene heterogeneity as seen in some other organisms (e.g., Harris and Crandall 2000; Parkin and Butlin 2004; Bower et al. 2008).

Phylogenetic analysis

The two genetic loci were subjected to Bayesian analysis using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Sequences were analyzed as a combined data

set, with each gene partitioned according to the general time-reversible model (Lanave et al. 1984) with invariant sites and gamma-distributed rate variation across sites (GTR+I+Γ) and with all parameters unlinked across loci. Bayesian analyses included four independent runs with three heated chains and one cold chain in each run. The MCMC chains were set for 3,000,000 generations and sampled every 100 generations; chains were run until the average standard deviation of the split frequencies dropped below 0.01. The burn-in period for each analysis was removed after graphical determination of stationarity.

RESULTS

Molecular Results

Genetic distances were low between individuals exhibiting the color form defined by having yellowish-brown integument, clear wings and orange pubescence on the metasoma (0% for ITS1 and 0.2% for ITS2: Table 1). Four of the five individuals exhibiting this color form had identical ITS1 and ITS2 sequences, so only one of these genetically identical individuals is included in Table 1. Genetic distances were also low among the form characterized by reddish-brown integument with clear wings and white pubescence on the metasoma (0.3% for ITS1 and 0.7% for ITS2: Table 1). The genetic distances were similar between the melanistic individuals (0.3% for ITS1 and 0.4% for ITS2: Table 1). Genetic distances were also relatively low between the Melanistic form and the Reddish-brown form with white pubescence (0.6%–1.10% for ITS1 and 0.5%–0.9% for ITS2: Table 1). The genetic distance between both forms with white pubescence and the form with orange pubescence was high (1.4%–1.7% for ITS1 and 1.9%–2.5% for ITS2: Table 1). These distances are as great as or greater than the genetic distance between any of the *S. unicolor* forms and the closely related species *S. angulifera* (0.9%–2.6% for ITS1 and 1.2%–2.5% for ITS2: Table 1). All sequences have been submitted to GenBank (Accession nos. GQ182985-GQ183013: Table 2).

Phylogenetic Results

Bayesian analysis of the combined molecular data produced a tree that clearly depicts the relationships among the color variants of *S. unicolor* and the outgroups (Fig. 1). This topology revealed three distinct clades that are separated from the outgroups by a relatively long branch length (large genetic distance). One clade is made up of *S. unicolor* specimens that have white pubescence on the metasoma, another is composed of *S. unicolor* specimens with orange pubescence on the metasoma, and the last clade is made up of *S. angulifera* specimens (Fig. 1). The relationships among these three clades are unclear, yet the distinctness of each is supported by a large posterior probability (1.0). While there was a separation between individuals with a reddish-black integument and those with a reddish-brown integument, the branch length separating these groups was small.

Morphological Results

Careful examination of numerous *S. unicolor* specimens revealed consistent morphological differences between the color form with dense fringes of orange setae on the margins of the tergites and the color form with dense fringes of white setae on the tergites. No consistent differences, besides integumental coloration, were found between the Reddish-brown form and the Reddish-black form. Among males, differences were found in the length and shape of the cuspis on the genitalia (Figs 2–5), as well as differences in setal coloration. Among females, differences were found in the size of the eyes, pygidial sculpture, as well as differences in setal coloration. While there were differences in integumental coloration in some of the male specimens, some had a reddish-black

Table 1. Genetic differences among the *Sphaeropthalma* species belonging to the *unicolor* species-group (ITS1 above diagonal, and ITS2 below).

		ITS1											
		S. mendica	*S. mendica*	*S. mendica*	*S. mendica* (melanistic)	*S. mendica* (melanistic)	*S. mendica* (melanistic)	*S. unicolor*	*S. unicolor*	*S. angulifera*	*S. angulifera*	*S. pinalea*	*S. triangularis*
ITS2	***S. mendica***	-	0.6%	0.3%	0.9%	1.2%	0.9%	1.8%	1.8%	2.7%	2.7%	9.0%	9.0%
	S. mendica	0.3%	-	0.3%	0.9%	1.2%	0.9%	1.8%	1.8%	2.7%	2.7%	9.0%	9.0%
	S. mendica	0.5%	0.8%	-	0.6%	0.9%	0.6%	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
	***S. mendica* (melanistic)**	0.4%	0.6%	0.6%	-	0.3%	0.0%	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
	***S. mendica* (melanistic)**	0.3%	0.5%	0.5%	0.4%	-	0.3%	1.8%	1.8%	2.7%	2.7%	8.6%	8.6%
	***S. mendica* (melanistic)**	0.3%	0.5%	0.5%	0.4%	0.3%	-	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
	S. unicolor	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	-	0.0%	0.9%	0.9%	7.6%	7.6%
	S. unicolor	1.8%	2.1%	2.1%	2.0%	1.8%	1.8%	0.3%	-	0.9%	0.9%	7.6%	7.6%
	S. unicolor	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.0%	0.3%	0.9%	0.9%	7.6%	7.6%
	S. unicolor	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.0%	0.3%	0.9%	0.9%	7.6%	7.6%
	S. unicolor	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.0%	0.3%	0.9%	0.9%	7.6%	7.6%
	S. angulifera	1.3%	1.6%	1.6%	1.4%	1.3%	1.3%	2.1%	2.4%	-	0.6%	7.3%	7.9%
	S. angulifera	NA	NA	NA	NA	NA	NA	NA	NA	NA	-	7.9%	7.9%
	S. pinalea	8.8%	9.1%	9.0%	8.9%	8.5%	8.8%	9.0%	9.3%	8.9%	NA	-	3.0%
	S. triangularis	9.0%	9.3%	9.3%	8.9%	9.0%	9.0%	9.3%	9.6%	9.1%	NA	5.6%	-

Table 2. Genbank Accession numbers and descriptive information about the velvet ant specimens used in the genetic analyses.

Species	Voucher ID	Collection Location	ITS1 Accession #	ITS2 Accession #
S. angulifera	JP276	CA, San Bernardino Co., 5.5 mi S Barstow	GQ182985	GQ183000
S. angulifera	JW04	UT, Washington Co., 3 mi West of Bloomington	GQ182986	NA
S. mendica	JP555	NV, Nye Co., Pahrump	GQ182990	GQ183004
S. mendica	JP556	UT, Garfield Co., Alvey Wash, 5 km S Escalante	GQ182991	GQ183005
S. mendica	JP625	UT, San Juan Co., Valley of the Gods	GQ182994	GQ183008
S. mendica	JP626	NM, San Juan Co., 3 mi S Farmington	GQ182995	GQ183009
S. mendica	JW12	UT, Garfield Co., Alvey Wash, 7 km S Escalante	GQ182998	GQ183012
S. mendica	KW08	CA, Riverside Co., Corn Springs	GQ182999	GQ183013
S. pinalea	JP761	AZ, Cochise Co., Carr Canyon	GQ182987	GQ183001
S. triangularis	JP108	AZ, Cochise Co., San Pedro Riparian Cons. Area	GQ182988	GQ183002
S. unicolor	JP102	CA, Riverside Co., Bautista Canyon	GQ182989	GQ183003
S. unicolor	JP557	CA, Kern Co., 10 mi WSW McKittrick	GQ182992	GQ183006
S. unicolor	JP558	CA, Solano Co., Stebbins Cold Canyon Reservoir	GQ182993	GQ183007
S. unicolor	JP712	CA, Solano Co., Suisun City, Rush Ranch	GQ182996	GQ183010
S. unicolor	JP97	CA, Riverside Co., Bautista Canyon	GQ182997	GQ183011

integument while others had reddish-brown, no differences in genitalia morphology were found.

An examination of *S. angulifera* revealed similar genitalic morphology to the color form of *S. unicolor* with dense fringes of orange setae on the margins of the tergites (Figs 2–5). Also, the mandibles of *S. angulifera* are different from those of any of the color forms of *S. unicolor*, with the base of the mandibles being wide, the dorsal carina terminating at ½ the distance from the base forming a lobe, and the presence of a small angulate ventral tooth.

Based on the above molecular and morphological data, we are recognizing *S. unicolor* and *S. mendica* as distinct species in the following taxonomic section.

Sphaeropthalma unicolor (Cresson)

Mutilla unicolor Cresson, 1865. Ent. Soc. Phila., Proc. 4: 389. Male. Lectotype data: California, type no. 1887 (ANSP).

Mutilla auraria Blake, 1879. Amer. Ent. Soc., Trans. 7: 248. Female. Holotype data: Nevada, type no. 4573 (ANSP).

Mutilla phaedra Blake, 1879. Amer. Ent. Soc., Trans. 7: 251. Female. Holotype data: Nevada, type no. 4575 (ANSP).

Agama rustica Blake, 1879. Amer. Ent. Soc., Trans. 7: 252. Male. Holotype data: California, type no. 4550 (ANSP).

Photopsis nebulosus Blake, 1886. Amer. Ent. Soc., Trans. 13: 275. Male. Holotype data: Nevada, type no. 4549 (ANSP).

Sphaerophthalmia (sic.) anthophora Ashmead, 1897. In: Davidson, South. Calif. Acad. Sci. Proc. 1: 5. Male Holotype data: California, Los Angeles, type no. 6113; Female Allotype data: California, Los Angeles, type no. 6113 (USNM).

Mutilla monochroa Dalle Torre, 1897. Cat. Hymen. 8: 63. New name for *M. unicolor* Cresson.

Dasymutilla sumneriella Cockerell, 1915. Entomologist 48: 259. Female. Holotype data: California, La Jolla, type no. 20409 (USNM)

Sphaeropthalma (Photopsis) rustica ocellaria Schuster, 1958. Ent. Amer. 37: 32. Male. Holotype data: California, Berkeley (UMSP).

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventrally with an indistinct basal tooth and an

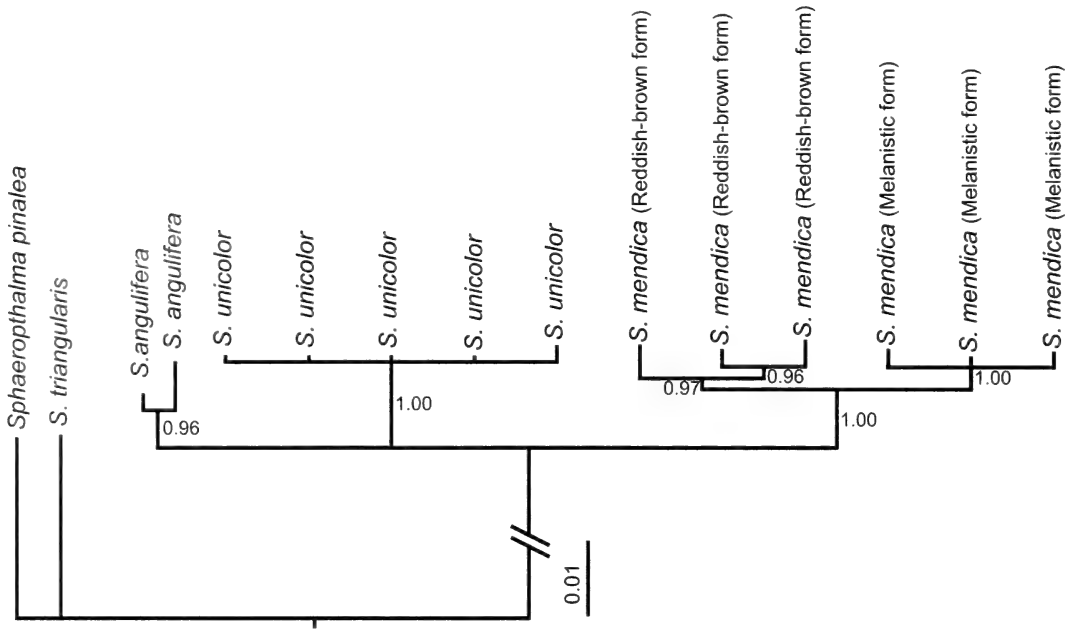


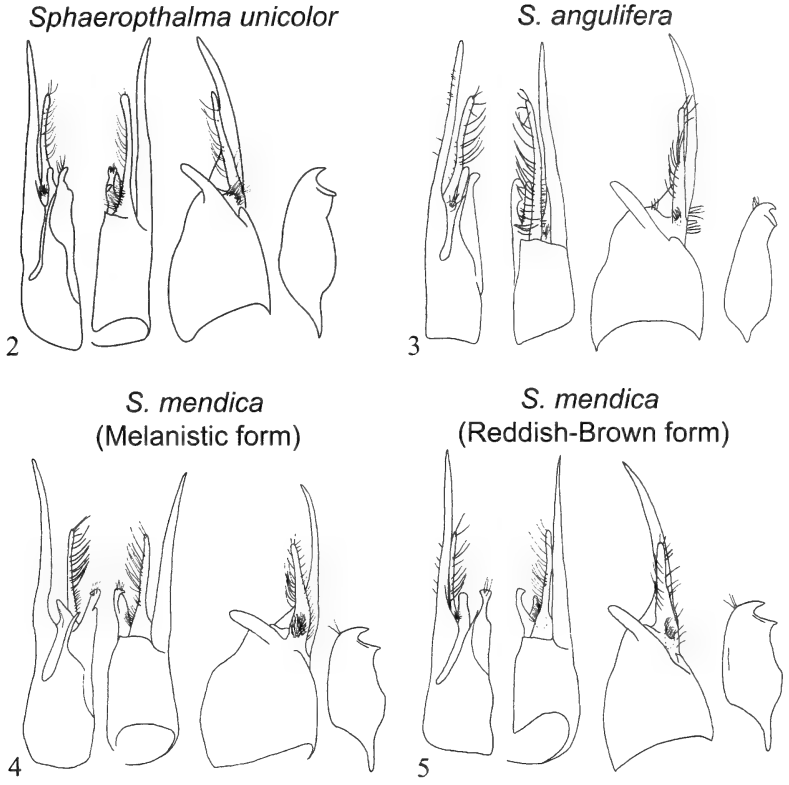
Fig. 1. Consensus tree of Bayesian analysis of the combined ITS1 and ITS2 sequences. Numbers at each branch represent posterior probabilities. Because a long branch separates the outgroup taxa from the ingroup taxa, we shortened this branch length; the genetic distance between the outgroup taxa and the ingroup taxa can be found in Table 1.

apex that is tridentate and oblique (Fig. 6), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. triangularis*, but the cuspis is only approximately 3/4 the free length of the paramere, rather than almost as long as the paramere (Fig. 2). The cuspis is a uniform diameter from the base to the apex (Fig. 2). This species has the apical margins of the tergites with dense fringes of orange plumose setae and often orange setae covering the head and mesosoma.

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eye length is less than the length from the posterior margin of the eye to the vertex of the head (the eye is from 0.85 to 0.92 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the tergites have dense fringes of orange plumose setae. Often, orange setae are covering the head and mesosoma as well.

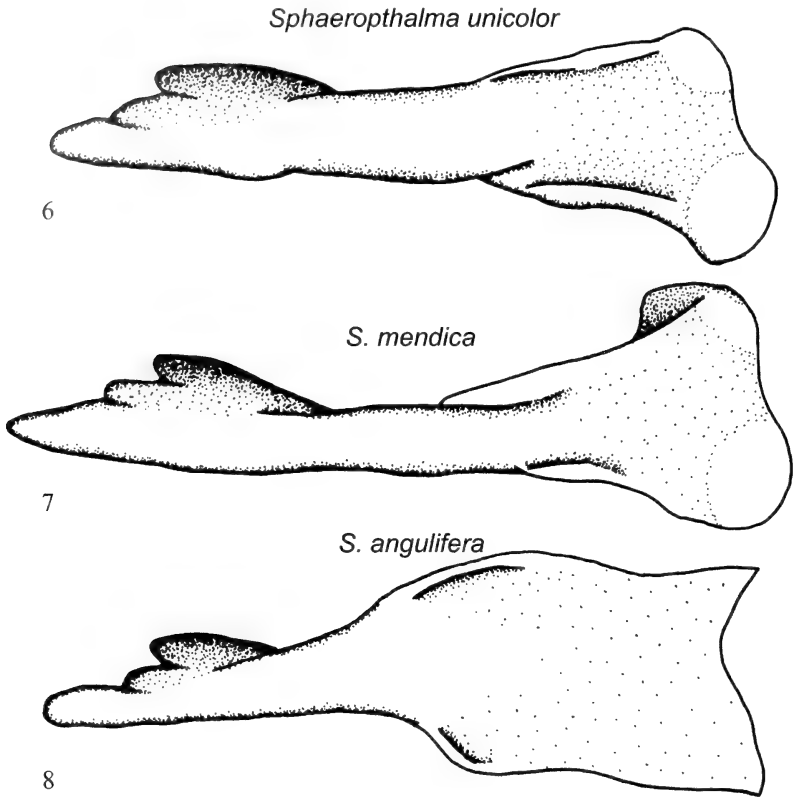
Distribution.—This species is common in the Central Valley of California and west of the Southern California Coastal Mountain Ranges. It is also present at the extreme western margin of the Great Basin Desert, along the foothills of the eastern side of the Sierra Nevada Range.

Material examined.—**MEXICO: Baja California**: Rancho sonora bampo, 54 mi S Tijuana, 3 ♂, 16.May.1959, J.A. Honey (LACM). **USA**: **California**: *Colusa Co.*: Colusa, 3 ♂, 15.Aug.1955, R. Schuster (UCDC); *Fresno Co.*: Fresno, 1 ♂, 28.May.1956, 2 ♂, 3.Jun.1956, Schuster (UCDC); Helm, 1 ♂, 26.Jul.1960, R.R. Snelling (LACM);



Figs 2–5. Genitalia: dorsal view left; ventral view right; internal lateral view, penial valve removed; penial valve, lateral view; 2. *Sphaeropthalma unicolor*; 3. *S. angulifera*; 4. *S. mendica* (Melanistic color form); and 5. *S. mendica* (Reddish-brown color form).

Little Panoche Reservoir, 4 mi W of I-5, 6 ♂, 27.May.2005, E.E. and K.A. Williams (KAWC); Parkfield, 2 ♂, 28.Sep.1968, E.A. Kane (LACM); *Lake Co.*: Soda Bay, 1 ♂, 17.Jul.1959, 4 ♂, 25.Jul.1958, R.E. Dolphin (UCDC); *Los Angeles Co.*: Big Rock Creek, San Gabriel Mts, 1 ♂, .Oct.1959, Honey and Sphon (LACM); Boquet Cyn, 1 ♂, 28.Jul.1938, 1 ♂, 23.Jul.1937, N. Westerland (LACM); Claremont, 1 ♀ (EMUS); Glendale, 1 ♂, 21.Jun.1951, W.M. Schlinger, 1 ♂, 11.Jul.1952, 1 ♂, 25.Aug.1954, 1 ♂, 29.Aug.1951, 1 ♂, Aug.1953, 1 ♂, 11.Sep.1949, 1 ♂, 10.Oct.1951, E.I. Schlinger (UCDC); 1 ♂, 1952, W.M. Schlinger (EMUS); Laurel Cyn, 1 ♂, 28.Jul.1968, B. Duff (LACM); Malibu, 1 ♀, 3.Jul.1950, D.R. Estes (EMUS); San dimas, 1 ♂, 1953 (LACM); San Gab Cyn, 1 ♂, 10.Jul.1965 (LACM); Tanbark Flat, San Gabriel Mts, 10 ♂, 7.Jul.1963, R.R. Snelling (LACM); Tanbark Flat, 15 ♂, 38 ♀, 21–25.Jun.1956, 1 ♂, 25.Jun.1956, A. Menke Jr., 1 ♂, 1.Jul.1950, J.D. Paschke, 1 ♂, 3.Jul.1950, H.L, Hansen, 2 ♂, 17.Jul.1956, R.G. Bechtel, 1 ♂, 17.Jul.1959, P.D. Hurd, 2 ♂, 19.Aug.1950, E.B. Goodwin, 3 ♂, 20.Aug.1950, E.B. Goodwin, 4 ♂, 2–3.Sep.1950, E.B. Goodwin, 2 ♂, 14.Sep.1950, E.B. Goodwin (UCDC); *Kern Co.*: Bakersfield, 1 ♂, 11.Jun.1968, E.A. Kane, 1 ♂, 11.Jul.1951, 1 ♂, 14.Jul.1951, 2 ♂, 18.Jul.1951, 1 ♂, 27.Jul.1951, I.W. Isaak (LACM); Maricopa, 22 mi S, Valle Vista Cpgrd., 5 ♂, 16.Sep.2004, E.E. and K.A. Williams (KAWC); Wasco, 26 ♂, 26.Jun.1951, 1 ♂, 27.Jun.1951, 1 ♂, 9.Jul.1951, L.W. Isaak (UCDC); Woody, 1 ♂, 15.Jul.1951, L.W. Isaak (UCDC); *Marin Co.*: Mill Valley, Lee Street, 2 ♂ 5–6.Aug.1966, 1 ♂, 30.Sep.1966, T.W. Davies (PMNH); *Merced Co.*: Livingston, 1 ♂, 30.Sep.1961, R. Howkswarth (LACM); *Monterey Co.*: San Ardo, 2 ♂, 24.Jul.1969, R.E. Doty (LACM); *Plumas Co.*: Greenville, 1 ♂, 11.Jul.1959, L.A. Stange (UCDC); *Riverside Co.*: Garner Valley, Kenworthy forest service station on Morris ranch rd., 2 ♂, 4.Jun.2002, M.E. Irwin and F.D. Parker (EMUS); Menifee Valley, hills on W end, 1 ♂, 23.Jul.1981, J.D. Pinto (UCRC);



Figs 6–8. Mandibles: 6. *Sphaeropthalma unicolor*; 7. *S. mendica*; and 8. *S. angulifera*.

San Timeteo Cyn, 4 ♂, 24–25.Sep.1969, M. Feigen and R. Hardy (LACM); The Gavilan, 1 ♂, 17.May.1951, E.L. Schlinger, R.G. Bechtel and E.J. Tayler (UCDC); UC Riverside, 1 ♂, 8–15.Oct.1979, J. Lasalle (UCRC); Winchester, 1 ♂, 5.Sep.1967, W. Icenogle (LACM); *San Bernardino Co.*: Camp O-ongo, nr running spr, San Bernardino Mtns, 2 ♂, 8–12.Aug.1966, C.L. Hogue (LACM); Meyer Can Rd, 5 mi NW Beuore, 5 ♀, 24–27.Sep.1975, M. Wasbauer (CSCA); *San Diego Co.*: dodge Valley, 1 ♂, 26.Mar.1958, E.I. Schlinger (UCDC); El Cajon, 4 mi S, 1 ♀, 27.Apr.1964, R. Ballard (EMUS); Rancho Santa Fé, 3 ♂, 4.Oct.1958, J. Northern (LACM); Scissors xing, 5.5 mi NW, 1 ♂, 8.Jul.1969, A.R. Hardy (LACM); *San Luis Obispo Co.*: Shandon, 1 ♂, 17.Sep.1968 (LACM); *Sacramento Co.*: Rio Linda, 3 ♂, 11.Jul.1959, J. Fowler (UCDC); *Santa Barbara Co.*: Painted Cave, 1 ♂, 7.Aug.1964, C.L. Remington (PMNH); Santa Cruz Island: UC reserve station, Cañada del Medio, 2 ♂, 30–31.Jul.1970, 1 ♂, 14.Aug.1968, 2 ♂, 19–29.Aug.1974, 1 ♂, 25–26.Aug.1971, 1 ♂, 10.Oct.1972, C.L. Remington (PMNH); Beecher's Bay, 1 ♂, 3–5.Oct.1972, L. Laughrin (PMNH); Toro Canyon Park, 1 ♂, 5–11.Oct.1999, R.L. Doutt (EMUS); *Shasta Co.*: Anderson, 2 ♂, Jul–Aug.1955, J. Willis (UCDC); Hat Creek; 1 ♂, 15.Jul.1955, Hogue (LACM), 1 ♂, 10.Jul.1955, 2 ♂, 16.Jul.1955, R.D. Browning, 1 ♂, 14.Jul.1955, E.I. Schlinger (UCDC); *Siskiyou Co.*: Weed, 5 mi SW, 3 ♂, 4 ♀, 9.Jun.2004, K.A. Williams (KAWC); *Sonoma Co.*: Mirabel Park, 1 ♂, 9–18.Aug.1962, C. Slobodchikoff (CISC); *Stanislaus Co.*: Del Puerto Cyn, 1 ♂, 13.Sep.2003, E.E. and K.A. Williams (KAWC); Stanislaus University, 2 ♂, 21.Oct.1905 (EMUS, LACM); *Tehama Co.*: Los Molinos, 1 ♂, 20.Jul.1956, 1 ♂ 24.Jul.1956, E. Yeomanr (UCDC); *Tuolumne Co.*: Strawberry, 1 ♂, 30.Jun.1951, C.A. Downing (UCDC); *Ventura Co.*: Anacapa Island, 2 ♂, 18.Aug.1940, C. Henne, 1 ♂, 23.Aug.1949, G.P. Kanakoff (LACM); *Yolo Co.*: Dunningan; 3.5 mi NW, 3 ♂, 17.Jun.1959, J. Fowler (UCDC); 4 mi SW, 1 ♂, 14.Jul.1959, 3 ♂, 28.Jul.1959, 1 ♂, 31.Jul.1959, 1 ♂, 4.Aug.1959, 1 ♂, 11.Aug.1959, J. Fowler (UCDC); 7 mi NW, 1 ♂, 15.May.1959, 3 ♂, 1.Jul.1959, 15 ♂, 12.Jul.1959, 5 ♂, 14.Jul.1959, 1 ♂, 15.Jul.1959, 5 ♂, 16.Jul.1959, 2 ♂, 21.Jul.1959, 2

♂, 22.Jul.1959, 2 ♂ 23.Jul.1959, 1 ♂, 28.Aug.1959, 3 ♂, 2.Sep.1959, 1 ♂, 29.Sep.1959, J. Fowler (UCDC); Rumsey, 1 ♂, 23.Jul.1955, 1 ♂, 5.aug.1955, E.A. Kurtis (UCDC); Winters, 8 mi NW, 1 ♂, 5.Jun.1959, 3 ♂, 22.Jun.1959, 3 ♂, 25.Jun.1959, 1 ♂, 1.Jul.1959, 1 ♂, 8.Jul.1959, 2 ♂, 13.Jul.1959, 1 ♂, 16.Jul.1959, 1 ♂, 5.Aug.1959, 1 ♂, 11.Aug.1959, 1 ♂, 28.Aug.1959, 4 ♂, 2.Sep.1959, J. Fowler (UCDC); Yolo, 3 mi NW, 1 ♂, 1.Jul.1959, J. Fowler (UCDC); Zamora, 9 mi W, 1 ♂, 28.Jul.1959, 1 ♂, 11.Aug.1959, J. Fowler (UCDC); *Yuba Co.*: Wheatland, 5 mi N, 1 ♂, 11.Sep.2000, B.L. Williams (KAWC). **Nevada,** *Carson City*: Carson City, Ash Cyn, 1 ♂, May–Sep.1981, J.B. Knight (NVDA); *Washoe Co.*: Thomas Creek, 1 ♂, 3.Aug.1972 (NVDA); Reno, 1 ♂, 5.Jun.1979, 1 ♂, 11.Jun.1979, R.C. Bechtel (NVDA); Washoe Lake State Park, 16 mi S Reno, 1 ♂, 1 ♀, 2.Aug.2005, K.A. Williams (KAWC). **Oregon**, *Grant Co.*: John Day, 1 ♀, 8.Oct.1971, O. Warger (PMNH). **Washington**, *Benton Co.*: Hanford Site, 1 ♂, 1.Sep.1995, R.S. Zack (EMUS); *Klickitat Co.*: Pot Hole lake, 1 ♀, 15.Jul.1963, D. Mays (PMNH)

Remarks.—While morphologically similar to *S. mendica*, *S. unicolor* can be easily recognized by color. The integument of *S. unicolor* is generally lighter than *S. mendica* and the setae are orange on the fringes of the tergites rather than white. In older specimens, the orange setae have often faded to a pale yellow, but are not white like the setae of *S. mendica*. The differences in color between these two species are consistent, yet there is some color variation among *S. unicolor* individuals. We have examined some individuals from the Central Valley of California that have a dark melanistic integument similar to some of the *S. mendica* specimens. However, these melanistic *S. unicolor* individuals retained the distinct setal coloration characteristic of the species. Female *S. unicolor* specimens range from having orange to dark red setae, which may explain why they have been confused for *Dasymutilla*.

Sphaeropthalma mendica (Blake), NEW STATUS

Agama mendica Blake, 1871. Amer. Ent. Soc., Trans. 3: 259. Male. Holotype data: Nevada, type no. 4551 (ANSP).

Mutilla aspasia Blake, 1879. Amer. Ent. Soc., Trans. 7: 250. Female. Holotype data: Nevada, type no. 4574 (ANSP). **New Synonym.**

Photopsis nebulosus Blake, 1886. Amer. Ent. Soc., Trans. 13: 275. Male. Holotype data: Nevada, type no. 4549 (ANSP). **New Synonym.**

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventrally with an indistinct basal tooth and an apex that is tridentate and oblique (Fig. 7), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. unicolor*, but the cuspis is approximately half the length of the parameres (Figs 4–5). The cuspis is nearly twice the diameter at the base compared to the diameter at the apex (Figs 4–5). This species has the apical margins of the tergites with dense fringes of white plumose setae and often white to orange setae covering the head and mesosoma.

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eyes are larger than the distance from the posterior margin of the eye to the vertex of the head (the eye is from 1.2 to 1.4 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the tergites have dense fringes of white plumose setae.

Distribution.—This species is widespread in the Mojave and Sonoran deserts. It is also present in the Great Basin Desert, the Colorado Plateau and the Snake River Plain.

Material Examined. **MEXICO: Baja California Sur**: Guerrero Negro, sand dunes 8 km N, 2 ♂, 8–9.Sep.1977, R.R. Snelling (LACM). **USA: Arizona**: *Cochise Co.*: Chiricahua Mtns., S. Cave Creek Cyn., 3 ♂ 11.Sep.1979, Knowlton, Hanson (EMUS); Huachuca Mtns., Ramsey Canyon, 1 ♂, 29.May.1964, B.F. Sternitzky (PMNH); Sierra Vista, 1 ♂, 16.Jun.1964, B.F. Sternitzky (PMNH); *Santa Cruz Co.*: Sycamore Cyn., Ruby Road, 2 ♂, 9.Sep.1979, Knowlton, Hanson (EMUS). **California**: *Imperial Co.*: Algodones Dunes: Niland-Glamis Road, 7.4 km NW Glamis, 1 ♂, 1–2.Jun.2008, Museum Survey Team (UCDC); *Inyo Co.*: Independence, 2 mi E, 3 ♂, 2.Jul.1968 (CSCA); Inyo Mtns, 12 mi E Big Pine, 1 ♀, 21.Aug.1982, D. Giuliani (EMUS); White Mtns., Grand View Camp, 1 ♂, 24.Jul.1982, N.J. Smith (UCDC); *Riverside Co.*: Corn Springs, 5 mi N Desert Center, 10 ♂, 21.May.2004, 18 ♂, 24.Jun.2004, K.A. Williams (KAWC); Deep Canyon Desert Research Center, 1 ♂, 2–5.Jun.2002, M.E. Irwin and F.D. Parker (EMUS); Wiley Well, 1 ♂ 12.Oct.1941, G.I. Virlett (LACM). **Idaho**: *Owyhee Co.*: Bruneau Dunes State Park, 1 ♂, 19.Jun.2008, J.S. Wilson and L.E. Wilson (EMUS). **Nevada**, *Clark Co.*: Corn Creek, 1 ♂, 18.Jun.1965, T.W. and W.T. Davies (PMNH); Willow Creek, 1 ♂, 14.Aug.1972, G.M. Nishida (NVDA); *Douglas Co.*: Pine Nut Creek, 1 ♂, 7.Aug.1972, G.M. Nishida (NVDA); *Esmeralda Co.*: Middle Creek, 1 ♂, 22.Jul.1971, G.M. Nishida (NVDA); *Lincoln Co.*: Beaver Dam St Prk, 1 ♂, 11.Aug.1971, D.F. Zoller (NVDA); Modena summit, 1 ♂, 28.Jul.1976, R.C. Bechtel, J.B. Knight and D.F. Zoller (NVDA); Oak springs summit, 8 ♂, 6–10.Aug.1974, G.M. Nishida and D.F. Zoller (NVDA); Pioche, 2 ♂, 6.Aug.1981, P.C. Bechtel (NVDA); *Lyon Co.*: Yerington, 3 mi E, 1 ♂, 8.Aug.1973, G.M. Nishida (NVDA); *Mineral Co.*: Whisky Flat, 1 ♂, 11.Jul.1979, R.C. Bechtel and R.L. Bradley (NVDA); *Nye Co.*: Beatty, 2.3 mi NW, 1 ♂, 15.May.1971 (CSCA); Nevada Test Site, 2 ♀, 22.Jul.1967, 1 ♀, 14.Jul.1967, 1 ♀ 31.Jul.1967, 2 ♀ 18.Aug.1967 (EMUS); Nellis AFB, Groom Lake Rd, 9.2 mi N, 1 ♀, 14.Jul.1967, 1 ♀, 24.Jul.1967 (EMUS); Nellis AFB, Groom Lake Rd, 11 mi N, 1 ♀, 8.Jul.1967, 1 ♀, 17.Jul.1967 (EMUS); Peavine Cyn, 1 ♂, 11.Aug.1967, C.D. Cooney (NVDA); *Storey Co.*: Virginia City highlands, 1 ♂, 11.Aug.1984, J.B. Knight (NVDA); *White Pine Co.*: Mt Hamilton, 1 ♀, 21.Jun.1974, L.V. Barclay (NVDA). **New Mexico**: *San Juan Co.*: Farmington, 3 mi S, 5 ♂, 10–11.Jun.2007, J.S. Wilson and L.E. Wilson (EMUS). **Utah**: *Emery Co.*: Gilson's Butte, 7 ♂, 20.Aug.2001, M.E. Irwin, F.D. Parker (EMUS); Goblin Valley State Preserve, 2 mi N, 18 ♂, 13 ♀ 25.Aug.1980, A.S. Menke F.D. Parker and K.A. Menke (EMUS); Hanksville, 16 mi N, 14 ♂, 1 ♀, 18.Sep.1980, Hanson and Knowlton (EMUS); Huntington, 2 ♂, 21.Jul.1940, F.C. Harmston (EMUS); Little Flat Top, 3 ♂, 22–26.Jul.2001, M.E. Irwin, F.D. Parker (EMUS); Little Gilson Butte: 2 mi W, 49 ♂, 7 ♀, 15–17.Sep.1980, Griswold, Parker and Veirs (EMUS); 4 ♂, 20–23.Jul.1981, Griswold, Parker and Veirs (EMUS); San Rafael Desert, nr Goblin Valley, 4 ♂, Sep.1980, G.E. Bohart (EMUS); Wild Horse Creek, N Goblin Valley, 6 ♂, 16–17.Sep.1980; 3 ♂, 21–23.Jul.1980, Griswold and Parker (EMUS); *Garfield Co.*: Buckskin spring, N Goblin Valley, 23 ♂, 2.Aug.1997, M.J. Wasbauer (UCDC); Escalante, 37 km SE, 29 ♂, 11.Aug.1997, M.J. Wasbauer (UCDC); Long Canyon, 4 ♂, 5–19.Jul.2003, H. Ikerd (EMUS); Shootering Cyn., 1 ♂, 1.Jul.1978, D. Vogt (EMUS); Starr Springs, 1 ♂, 27.Aug.1971, D.F.H. (EMUS); Wild Horse Creek, N Goblin Valley, 7 ♂, 5.Aug.1997, M.J. Wasbauer (UCDC); *Grand Co.*: Moab, 13 mi W, 1 ♂, 26.Aug.1971 (EMUS); *San Juan Co.*: Lime creek, 1 ♂, 13.Jul.1967, S. Waldron (EMUS); *Uinta Co.*: Bonanza, SW, 1 ♂, 30.Jul.1978, G.E. Bohart; 2 ♂, 3.Aug.1981, 2 ♂, 11.Aug.1981, 1 ♂, 28.Aug.1981, M. Schwartz and R. Miller (EMUS); Vernal, 19.Jul.1941, 3 ♂, G.F. Knowlton (EMUS); White River, 3 mi S Bonanza, 3 ♂, 10.Aug.1964, B and C Durden (PMNH). *Washington Co.*: Leeds, 1 ♀, 13.Jun.1961, D.W. Davis (EMUS); Leeds, Oak Grove CG, 1 ♀, 8.Jun.1964, D.W. Davis (EMUS); *Wayne Co.*: Hanksville, 14 mi S, 5 ♂, 25.Jul.1978, Hardy and Andrews (CSCA).

Remarks.—There is a wide array of integumental coloration in this species. Specimens range from nearly black integument to a more reddish-brown color characteristic of most nocturnal mutillids. Female integumental coloration has a similar range as the males. The setal coloration rarely varies among *S. mendica* specimens. Some individuals have pale orange setae on their mesosoma, but the majority has entirely white setae. All specimens have dense fringes of white

plumose setae on the apical margins of the tergites. Female *S. mendica* specimens often appear less setose than females of *S. unicolor*.

Sphaeropthalma angulifera Schuster

Sphaeropthalma (*Photopsis*) *angulifera* Schuster, 1958. Ent. Amer. 37: 32. Male. Holotype data: California, Kern Co., Bakersfield (CASC).

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventrally with a distinct angulate basal tooth and an apex that is tridentate and oblique, but most importantly the dorsal carina of the mandible is angulate at the midpoint of the mandible coinciding with the ventral tooth (Fig. 8), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. unicolor* (Fig. 3). The cuspis is a uniform diameter from the base to the apex (Fig. 3).

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with moderately dense erect pale golden brachyplumose setae that do not obscure the integument; the ventral margin of the mandible has a slight excision followed by a distinct angulate tooth; the head below the eyes widens towards the mandibular insertions; the first metasomal segment is sessile with the second; the pygidium is granulate; and the apical margins of the tergites have dense fringes of white plumose setae.

Description of female: Coloration and setal pattern. Body testaceous. Legs and flagellum lighter. Moderately dense pale golden brachyplumose setae throughout; integumental sculpture visible. Metasomal segments with dense fringe of white plumose setae. Legs with white brachyplumose setae.

Head. Head rounded posteriorly, not as wide as mesosoma, moderately punctate. Width of face at mandibular base wider than width immediately ventral to eyes. Eye ovate, distance from posterior mandibular articulation ~2.5X visible length of pedicel. Clypeus protruding anteriorly, posteromedially produced into low triangular tubercle. Antennal scrobe with indistinct dorsal carina. Antennal tubercle glabrous. Flagellomere I ~1.3X length of pedicel. Flagellomeres II–III ~1.0–1.1X length of pedicel. Mandible bidentate apically. Ventral mandibular margin with slight angulate basal tooth; dorsal margin with incomplete carina ending at basal third of mandible, not produced apically as tubercle. Genal carina absent.

Mesosoma. Mesosoma slightly wider anteriorly than posteriorly, slightly longer than broad. Mesosoma coarsely punctate on dorsum. Propleuron anteriorly, mesopleuron medially running vertically, and extreme ventral region of propodeal side punctate. Humeral angle dentate. Scutellar scale absent. Mesosternum with low transverse tubercle present medially just anterior to mesocoxa. Metasternum tridentate. Propodeum with distinct dorsal and vertical faces; lateral face impunctate.

Metasoma. Segment 1 distinctly sessile with segment 2. T1 with small sparse punctures. Tergite 2 with sparse shallow punctures. T2 with felt line; length 0.2X length of tergite. T3–5 shagreened. T6 with distinct pygidial area defined by weak carinae; surface strongly densely granulate. S2–5 with punctation similar to tergites.

Length. ~6.4–11 mm.

Distribution.—This species is found in the Mojave and Western Sonoran deserts.

Material examined.—**USA: California:** *Kern Co.*: Maricopa, 5 mi SW, 3 ♂, 16.Sep.2004, EE & KA Williams (KAWC); *San Bernardino Co.*: Lucerne Valley, 10 mi SE, 3 ♂, 16.Sep.2004, EE & KA Williams (KAWC); *Inyo Co.*: Olancha, 3 mi NE, Sand Dunes, 3.Jul.2005, 1 ♂, KA Williams (KAWC); Olancha, 4 mi NE, Dirty Socks Hot Springs, 3.Jul.2005, KA Williams (KAWC); **Nevada:** *Nye Co.*: Mercury, 1 ♂, 4.May.1961, 1 ♀, 8.May.1961, 1 ♀, 19.May.1961, 1 ♀, 1.Jun.1961,

1 ♂, 19.Jun.1961, 1 ♀, 20.Jun.1961, 1 ♂, 21.Jun.1961, 1 ♀, 22.Jun.1961, 1 ♀, 6.Jul.1961, 1 ♂, 21.Jul.1961 (BYUC). **Utah:** *Washington Co.*: Leeds Canyon, 1 ♂, 17.Jul.1980, Hanson, Knowlton & Clemons (EMUS); Zion National Park, 1 ♂, 23.Jul.1978, 1 ♂, 22.Sep.1978, Gafney (EMUS).

Remarks.—While *S. angulifera* is morphologically similar to *S. unicolor* and *S. mendica*, it can easily be differentiated from these two species. There is little variation in the integumental coloration of *S. angulifera*, most specimens are a yellowish-brown, similar to the majority of nocturnal mutillids. No differences were found in setal coloration of this species, all specimens are clothed with orange setae on the apical margins of the tergites.

The sex association is based on similarities of the female to that of *S. mendica* and distributional data. Ferguson (1967) collected both *S. mendica* and *S. angulifera* at the Nevada Test Site. After studying the morphology of an unknown set of females, he decided that they appeared to be closely related to *S. mendica*. The only closely related species at the Test Site was *S. angulifera*, which happened to be known only from the male. He concluded that these two sexes must be conspecific, but never published this information. We agree with his conclusions.

DISCUSSION

Molecular tools are becoming increasingly important in deciphering cryptic or morphologically challenging species complexes (Pilgrim and Pitts 2006; von Dohlen et al. 2006; Pitts et al. 2007; Wilson and Pitts 2008). Our analysis of *S. unicolor* uncovered the existence of two sister species, *S. angulifera* and *S. mendica*, the latter being previously unrecognized. After a thorough morphological analysis of these species, multiple traits were discovered that support the molecular data.

While relatively large genetic distances separate these species (Table 1), the intraspecies variation differs between species. Populations of *S. unicolor*, for example, all have nearly identical ITS1 and ITS2 sequences, being separated only by small genetic distances (Table 1). This suggests that there is gene flow between populations of *S. unicolor*. Populations of *S. mendica*, however, are separated by larger genetic distances (Table 1), which suggests reduced or no gene flow is occurring between some populations. Genetic distances among populations of *S. mendica* that exhibit the same color morph are also somewhat large (Reddish-brown form: 0.3% for ITS1 and 0.7% for ITS2; Melanistic form: 0.3% for ITS1 and 0.4% for ITS2). These distances are slightly lower than the genetic distances between the Reddish-brown form and the Melanistic form of *S. mendica* (0.6%–1.1% for ITS1 and 0.5–0.9% for ITS2). This suggests that the two color morphs rarely, if ever, interbreed. But, because only few individuals were analyzed, more data are needed to determine the amount of gene flow between these color forms. It is likely that additional specimens, from a broader geographic region, could show that there is no significant genetic difference between these two forms. Because of the low genetic distance, coupled with the lack of morphological differentiation, between color morphs of *S. mendica*, we feel that, until more data can be gathered that suggests otherwise, these color forms should be considered the same species.

Ferguson (1967) suggested that the Melanistic form of *S. mendica* was geographically isolated from the Reddish-brown form by elevation, with the darker form being found only above 5,500 ft. We found this not to be the case. We have collected the Melanistic form of *S. mendica* at elevations ranging from 2,500 ft in southern Idaho, to 6,000 ft in southern Utah. Also, we have collected the Reddish-brown form at elevations ranging from 1,600 ft in the Sonoran Desert to 6,600 ft in southern Utah. While there does seem to be a phylogenetic split between these color forms (Fig. 1), it is not easily explained by elevation. Differences in integumental col-

oration do not appear to suggest species-level differences in *S. mendica*. It is possible that the differences seen in this species are due to humidity differences during development as Ferguson (1962) suggested, but more research must be done before this conclusion can be made.

Setal coloration in some mutillid wasps (e.g., *Dasymutilla*) is variable within a single species and is, therefore, not always reliable to diagnose species (Pilgrim et al. 2009). The differences in setal coloration between *S. mendica* and *S. unicolor* are, however, consistent and useful in diagnosing these two species. Differences in color, without any additional structural differences, should rarely be used to differentiate between species. Researchers must use caution when describing new species based solely on differences in color. When these color differences are also supported by structural and/or genetic differences, color can be a useful and easy way to diagnose species.

ACKNOWLEDGMENTS

We thank Kevin Williams and David Tanner (Utah State University, Logan, UT), for their thoughtful and helpful comments regarding this manuscript. We would like to thank Erik Pilgrim, Carrie Drake, Kevin Williams, and Carol von Dohlen for help with the molecular aspect of this study. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah. Approved as journal paper no. 8078.

LITERATURE CITED

Bower, J. E., M. Dowton, R. D. Cooper, and N. W. Beebe. 2008. Intraspecific concerted evolution of the rDNA ITS1 in *Anopheles farauti* Sensu Stricto (Diptera: Culicidae) reveals recent patterns of populations structure. *Journal of Molecular Evolution* 67: 397–411.

Ferguson, W. E. 1962. Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values (Hymenoptera). *University of California Publications in Entomology* 27: 1–92.

———. 1967. Male sphaeropthalmine mutillid wasps of the Nevada Test Site. *Brigham Young University Science Bulletin, Biological Series* 8: 1–26.

Harris, D. J. and K. A. Crandall. 2000. Intragenomic variation within ITS1 and ITS2 in freshwater crayfishes (Decapoda: Cambaridae): Implications for Phylogenetics and microsatellite studies. *Molecular Biology and Evolution* 17: 284–291.

Lanave, C., G. Preparata, C. Saccone, and G. Serio. 1984. A new method for calculating evolutionary substitution rates. *Journal of Molecular Evolution* 20: 86–93.

Manley, D. G. 2003. Descriptions of males of three species of *Dasymutilla* Ashmead (Hymenoptera: Mutillidae) from California, with their sex associations. *Pan-Pacific Entomologist* 79: 1–10.

——— and J. P. Pitts. 2007. Revision of the Neotropical velvet ants of the genus *Dasymutilla* (Hymenoptera: Mutillidae). *Zootaxa* 1487: 1–128.

——— and K. A. Williams. 2005. A New Color Variant of *Dasymutilla atricauda* Mickel from Imperial County, California (Hymenoptera: Mutillidae). *Pan-Pacific Entomologist* 81: 184–185.

Mickel, C. E. 1924. A revision of the mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* occurring in America North of Mexico. *Proceedings of the U.S. National Museum* 64: 1–51.

———. 1928. Biological and taxonomic investigations on the mutillid wasps. *United States National Museum Bulletin* 143: 1–351.

———. 1935. Descriptions and records of mutillid wasps of the nerera *Myrmilloides* and *Pseudomethoca* (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 61: 383–398.

———. 1936. New species and records of nearctic mutillid wasps of the genus *Dasymutilla* (Hymenoptera). *Annals of the Entomological Society of America* 29: 29–60.

———. 1939. A monograph of the Neotropical mutillid genus *Hoplomutilla* Ashmead (Hymenoptera: Mutillidae). *Revista de Entomologia, Rio de Janeiro* 10: 337–403.

———. 1941. Monograph of the South American genus *Hoplocrates* Mickel (Hymenoptera: Mutillidae). *Revista de Entomologia, Rio de Janeiro* 12: 341–414.

———. 1943. The South American genus *Atillum* André (Hymenoptera: Mutillidae). *Revista de Entomologia, Rio de Janeiro* 14: 174–254.

———. 1960. A review of the mutillid genus *Cephalomutilla* (Mutillidae: Hymenoptera). *Revista de Brasil Entomologia, Sao Paulo* 9: 157–168.

Parkin, E. J. and R. K. Butlin. 2004. Within- and between-individual sequence variation among ITS1 copies in the Meadow Grasshopper. *Molecular Biology and Evolution* 21: 1595–1601.

Pilgrim, E. M. and J. P. Pitts. 2006. A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 79: 222–230.

———, K. A. Williams, and J. P. Pitts. 2008. Sex association and synonymy in Southwestern U.S. species of *Dasymutilla* (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 84: 58–69.

———, K. A. Williams, D. G. Manley, and J. P. Pitts. 2009. Addressing the *Dasymutilla quadriguttata* species-group and species-complex (Hymenoptera: Mutillidae): several distinct species or a single, morphologically variable species? *Journal of the Kansas Entomological Society, accepted.*

Pitts, J. P. 2006. Review of the *Sphaeropthalma imperialis* species-group (Hymenoptera: Mutillidae), with descriptions of females and taxonomic notes. *Zootaxa* 1248: 1–20.

———, J. S. Wilson, K. A. Williams, and N. F. Boehme. 2009. Velvet Ants (Hymenoptera: Mutillidae) of the Algodones Sand Dunes of California, USA. *Zootaxa, accepted.*

———, T. J. Boud, and E. M. Pilgrim. 2007. Molecular sex association of three species of nocturnal velvet ant (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 80: 136–145.

Ronquist, F. and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Schuster, R. M. 1958. A revision of the sphaeropthalmine Mutillidae of America north of Mexico. II. *Entomologica Americana* 37: 1–130.

Sheppard, P. M., J. R. G. Turner, K. S. Brown, W. W. Benson, and M. C. Singer. 1985. Genetics and the Evolution of Muellerian Mimicry in *Heliconius* Butterflies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 308: 433–610.

von Dohlen, C. D., C. A. Rowe, and O. E. Heie. 2006. A test of morphological hypotheses for tribal and subtribal relationships of Aphidinae (Insecta: Hemiptera: Aphididae) using DNA sequences. *Molecular Phylogenetics and Evolution* 38: 316–329.

Williams, K. A. and D. G. Manley. 2006. A New Color Variant of *Dasymutilla gloriosa* (Saussure) from Mexico (Hymenoptera: Mutillidae). *Pan-Pacific Entomologist* 82: 103–104.

——— and J. P. Pitts. 2008a. New species of predominately temperate velvet ant genera *Lomachaeta* Mickel and *Sphaeropthalma* Blake from Central America and northern South America (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 133: 297–326.

——— and J. P. Pitts. 2008b. Three Species Masquerading as One: Updating the Taxonomy of *Pseudomethoca russeola* and *P. donaeanae* (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 17: 127–133.

Wilson, J. S. and J. P. Pitts. 2008. Revision of Velvet Ant Genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by Using Molecular and Morphological Data, with Implications for Desert Biogeography. *Annals of the Entomological Society of America* 101: 514–524.

J. HYM. RES.
Vol. 18(2), 2009, pp. 227–243

Eight New species of *Lomachaeta* Mickel and the Synonymy of *Smicromutilla* Mickel (Hymenoptera: Mutillidae)

KEVIN A. WILLIAMS AND JAMES P. PITTS

Utah State University, Department of Biology, Logan, Utah 84322, USA;
KAW email: kawilliams@biology.usu.edu

Abstract.—*Smicromutilla* Mickel is determined to be a junior synonym of *Lomachaeta* Mickel. *Lomachaeta powelli* Mickel, **comb. nov.**, and *L. beadugrimi* Pitts & Manley, **comb. nov.**, are transferred from *Smicromutilla*. Eight new species of *Lomachaeta* are described: *L. hedera* **sp. nov.**, *L. ilex* **sp. nov.**, *L. litosisyra* **sp. nov.**, *L. megomicron* **sp. nov.**, *L. polemomechana* **sp. nov.**, *L. snellingella* **sp. nov.**, *L. theresa* **sp. nov.**, and *L. vacamuerta* **sp. nov.** *Lomachaeta garm* Williams & Pitts is a **junior synonym** of *L. hyphantria* Pitts & Manley. A revised key to the male species of *Lomachaeta* is provided. New distribution records are given for *L. chionothrix* Pitts & Manley, *L. hyphantria* Pitts & Manley, and *L. ptilohyalus* Pitts & Manley. Male genitalia are illustrated for all new species and the genitalia of *L. powelli* are illustrated for the first time.

Key words.—velvet ant, Sphaeropthalminae, parasitoid, Diodontus, Pisonopsis, Solierella, Trypoxylon

Species of *Lomachaeta* are rarely collected using traditional hand-collecting methods, mainly because of their small size (pers. obs.). Even in Malaise traps, *Lomachaeta* males appear to be especially rare in the eastern United States (Pitts and Manley 2004). In southwestern Nearctic regions, however, males of *Lomachaeta* can be more abundant in Malaise traps, although the females are rarely seen in these traps and are even less commonly hand-collected. Males and females are more reliably collected by rearing them from the nests of their hosts, which are typically small, twig-nesting crabronid wasps [e.g.: *Pisonopsis birkmani* Rowher, *Solierella blaisdelli* (Bridwell), *S. plenoculoides similis* (Bridwell), and *Trypoxylon sp.* Latreille] (Pitts and Manley 2004).

Mickel (1936) originally described *Lomachaeta* to include four species from the southwestern United States: one species from females only, two from males only, and one (type species, *L. hicksi* Mickel) from both sexes. Mickel (1940) added two more Southwestern species to *Lomachaeta*, bringing the total to six. Later a genus closely related to *Lomachaeta*, *Smicromutilla*, was described for the males and females of a single Californian species (Mickel 1964). Casal (1969) described the first two South American *Lomachaeta* species from females only with both species occurring in Argentina. Females of *Lomachaeta* were defined by a combination of characters seen in other mutillid genera, rather than by the unique tergal bristles seen in males. Because no males had been found in South America and females were not distinctive, the generic designation of the Argentine females was debatable. Quintero and Cambra (1996) discovered *Lomachaeta* specimens from Peru during a preliminary faunal study, but, because they were not described, the status of Neotropical *Lomachaeta* remained dubious.

The first revision of the genus was completed by Pitts and Manley (2004). They determined that all of Mickel's *Lomachaeta* species were synonymous, and discovered that the genus ranged throughout the Nearctic region. They described six

new *Lomachaeta* species, discovering males of the first undeniable species in South America, and one new *Smicromutilla* species. This species of *Smicromutilla* was difficult to place as it did not quite fit either genus, but, instead of erecting another monotypic genus, the species was tentatively placed into *Smicromutilla*. Finally, Williams and Pitts (2007) described one new *Lomachaeta* species from Colombia, partially addressing the somewhat disjunct range of the genus, which was previously unknown from northern South America.

Mickel (1964) used numerous characters to separate *Lomachaeta* and *Smicromutilla* when he first described them, and these characters have been used with limited success since then. Some of the subsequently described species (e.g. Casal 1969; Pitts and Manley 2004), and newly discovered species (to be described in this publication) do not fit the combinations of characters used to diagnose these genera. These discoveries necessitate a revision of taxonomic status for *Lomachaeta* and *Smicromutilla*.

Additionally, while studying material from various museums in search of small *Pseudomethoca* males to be used in a separate publication, eight new species were discovered that appear to be intermediate between *Lomachaeta* and *Smicromutilla*. Nearly all of these males are between 3mm and 6mm in length, and almost all were misidentified as *Pseudomethoca athamas* (Fox), *P. gila* (Blake), or *P. toumeyi* (Fox). These new species are described in the genus *Lomachaeta* below.

MATERIALS AND TERMINOLOGY

The following acronyms are used for institutions housing the material discussed in the current study:

CASC Department of Entomology, California Academy of Sciences, San Francisco, California, USA.

CDFA California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California, USA.

CISC Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, California, USA.

CNCI Canadian National Collection, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.

EMUS Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.

FSCA Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida, USA.

IAvH Instituto Alexander von Humboldt, Villa de Leyva, Colombia.

LACM Insect Collection, Los Angeles County Museum of Natural History, Los Angeles, California, USA.

UAIC Department of Entomology Collection, University of Arizona, Tucson, Arizona, USA.

UCDC The Bohart Museum of Entomology, University of California, Davis, California, USA.

UCRC UCR Entomological Teaching and Research Collection, University of California, Riverside, California, USA.

UMSP University of Minnesota Insect Collection, Department of Entomology, St. Paul, Minnesota, USA.

We have used the term "simple pubescence" for setae that are smooth and do not have barbed surfaces. "Brachyplumose pubescence" refers to setae with barbs that are less than or equal to the diameter of the shaft at the attachment of the barb. We have used the abbreviations T2, T3, etc., to denote the second, third, etc., metasomal

tergites while S2, S3, etc., denote the second, third, etc., metasomal sternites. Sparse punctures are separated by more than 2X the width of each puncture; moderately spaced punctures are separated by 1-2X the width of each puncture; dense punctures are separated by less than 0.5X the width of each puncture.

The illustrations in this manuscript were made using a camera lucida attached to a compound microscope at 100x magnification. Each illustration represents an internal-lateral view of the male genitalia, excluding the basal ring. To accomplish this, the genital capsule was first removed from each specimen using a narrow insect pin with an apical hook. Using this tool, in conjunction with a pair of fine-tipped forceps, the basal ring was removed, the lateral halves of the genitalia were separated, and the penis valve was removed. Lateral illustrations were made of the penis valve and remaining genital capsule. Because of the small size of these insects, some species may have short setae that were not observed in the illustration process. Finally, because of the angle of illustration, some figures appear to be less densely setose than the intact genitalia will appear in curated specimens.

Lomachaeta Mickel, 1936

Lomachaeta Mickel 1936: 289. Type species: *Lomachaeta hicksi* Mickel, by original designation.

Smicromutilla Mickel 1964: 108. Type species: *Smicromutilla powelli* Mickel, by original designation. **Syn. nov.**

Diagnosis.—Males of this genus can be separated from all other New World Mutillidae by the following unique combination of characters: the axillae are strongly dentate (Pitts and Manley 2004: Fig. 13); brachyplumose setae are present on the genae and pronotum; and the metasoma is subsessile or disciform, but never petiolate. Females of this genus possess the following combination of characters: the pygidium is undefined laterally and typically glabrous; the mesosoma is pyriform in shape, lacking lateral emargination anterior to propodeal spiracle; and the metasoma is narrow and either subsessile or disciform, but never broadly sessile or petiolate.

Distribution.—Throughout the Western Hemisphere, from Canada to Argentina

Remarks.—When Mickel (1964) first described *Smicromutilla*, he recognized its close relation to *Lomachaeta*. For males, *Smicromutilla* was separated from *Lomachaeta* by the absence of a ventral mandibular tooth, the absence of bristles on the margin of the second tergite, and the reduced wing venation. *Smicromutilla* females had the anterior and posterior spiracles unarmed, while those of *Lomachaeta* were tuberculate. Casal (1969) discovered female *Lomachaeta* from Argentina that had the propodeal spiracles tuberculate and the pronotal spiracles unarmed, displaying intermediate morphology between the known females of *Lomachaeta* and *Smicromutilla*. Pitts and Manley (2004) described five new male species of *Lomachaeta*; three of these species lack a ventral mandibular tooth, further blurring the line between *Lomachaeta* and *Smicromutilla*. Additionally, Pitts and Manley (2004) described one new *Smicromutilla* species that had normal wing venation. With the discovery of these species, the only characters that could be used to separate male *Smicromutilla* and *Lomachaeta* were the presence of bristles on T2 of *Lomachaeta* and the shape of the petiole, which is disciform in *Lomachaeta* and subsessile in *Smicromutilla* (Pitts and Manley 2004).

One specimen of *Lomachaeta ptilohyalus* Pitts & Manley from Yuma, Arizona lacks thickened bristles on the fringe of T2, although other known specimens of *L. ptilohyalus* have well-defined tergal bristles. Additionally, a new species (described here) from Mexico was discovered that has tergal bristles, like *Lomachaeta*, but a subsessile petiole, as in *Smicromutilla*. Because there are no consistent morphological

characters that can distinguish males of these two genera, and because it is doubtful that female morphology will provide generic-level characters given the limited number of differences known thus far, we consider *Smicromutilla* as a junior synonym of *Lomachaeta*.

Many of the new species were initially identified as *Pseudomethoca* Ashmead and, at first glance, can be easily confused with this genus. *Lomachaeta*, however, can easily be separated from *Pseudomethoca* by the dentate axillae (Pitts and Manley 2004: Fig. 13); *Pseudomethoca* have unarmed axillae. Because of the superficial similarity in appearance between these two genera, there are likely numerous specimens of *Lomachaeta* in the hastily sorted pseudomethocine material of many research collections.

Species-groups.—The males of *Lomachaeta* can be separated into two species groups based mainly on mandibular morphology: the *L. crocopinna* species-group, and the *L. hicksi* species-group.

The *L. hicksi* species-group is defined by the presence of a ventral mandibular tooth (as in Pitts et al. 2009: Fig. 46) and the presence of thickened, dark-brown or black bristles on the apical fringe of T2 (e.g. Fig. 19). The members of this species-group have fairly conserved genitalic morphology, but there is variation in the number of teeth on the penis valve (Pitts and Manley 2004: Figs 14–18). This species-group is found throughout North America, ranging from Massachusetts west to Oregon and south to Costa Rica. The species-group includes *L. chionothrix* Pitts & Manley, *L. cirrhomeris* Pitts & Manley, and *L. hicksi* Mickel.

The *L. crocopinna* species-group is defined by the lack of a ventral mandibular tooth. Most members of this species-group have only simple setae on the apical fringe of T2 and those with thickened bristles typically have pale yellow to orange-brown bristles. The members of this species-group have considerably different genitalic morphology, including differences in paramere shape and setae (Figs 1, 3, 5, 9, 11, 13, 15, and 17). This species-group ranges from California east to Texas and south to Argentina. Pitts and Manley (2004) had placed *L. hyphantria* into its own species-group based on differences in brachyplumose setae, mesonotal punctation, and setae of the parameres. We place the following 13 species into the *L. crocopinna* species-group, which is made up of: *L. beadugrimi* (Pitts & Manley), *L. crocopinna* Pitts & Manley, *L. hedera*, **sp. nov.**, *L. hyphantria* Pitts & Manley, *L. ilex*, **sp. nov.**, *L. litosisyra* **sp. nov.**, *L. megomicron*, **sp. nov.** *L. polemomechana*, **sp. nov.**, *L. powelli* (Mickel), *L. ptilohyalus* Pitts & Manley, *L. snellingella*, **sp. nov.**, *L. theresa*, **sp. nov.**, and *L. vacamuerta*, **sp. nov.** This is the largest and most morphologically variable species-group; future phylogenetic studies may recognize this group as paraphyletic.

Lomachaeta beadugrimi (Pitts & Manley, 2004), new combination

Smicromutilla beadugrimi Pitts & Manley 2004: 20. Holotype male: USA, California, San Bernardino Co., Granite Mts., 9.VI.1980, T. Griswold (EMUS). **Comb. nov.**

Diagnosis.—This species can be separated from all other *Lomachaeta* by the shape of the parameres, which are dorsoventrally flattened and rounded apically, and by the integument of T2, which is orange or red. The following characters are also useful for identification: the mandible is unarmed ventrally and the apical fringe of T2 lacks thickened bristles.

Genitalia: See Pitts and Manley (2004: 21, 26).

Length.—3–6 mm.

Female.—Unknown.

Host.—Unknown.

Material examined.—**USA:** CALIFORNIA: *San Bernardino Co.*: Kelbaker Road, 1 ♂, 17.May.2003, D. Yanega coll. (UCRC); Kelso Dunes Rd., 2 ♂, 17–18.May.2003, D. Yanega coll. (UCRC); Kramer Hills, 4 ♂, 14.May.2005. D. Yanega coll.

(UCRC); Lucerne Valley, vic., 1 ♂, 5.May.2001, G.R. Ballmer coll. (UCRC); 15 mi. NW of Yucca Valley, 1 ♂, collector and date unknown (UCRC).

Distribution.—California and Nevada.

Remarks.—This species has similar genitalia to *Lomachaeta snellingella,* **sp. nov.** (Fig. 13), but can easily be separated from it by the bright orange or red metasomal integument.

Lomachaeta chionothrix Pitts & Manley, 2004

Lomachaeta chionothrix Pitts & Manley 2004: 6. Holotype male: Guatemala, Zacapa, Rio Hondo, 7.VI.1987, collector unknown (CNCI).

Diagnosis.—This species can be separated from all other *Lomachaeta* by the following combination of characters: the mandible has a well-defined ventral tooth, the mesonotum is densely and deeply punctured, the legs are black, the apical fringe of T2 has thickened bristles (e.g. Fig. 19), and the penis valve of the genitalia is bidentate apically (see Pitts and Manley 2004: 26, fig. 14).

Genitalia: See Pitts and Manley (2004: 7, 24, 26).

Length.—3–6 mm.

Female.—Unknown.

Host.—Unknown.

Material examined.—**COSTA RICA:** GUANACASTE: 14 km S Cañas, EJN: F. D. Parker coll.: 2 ♂, 7–10.Mar.1989; 1 ♂, 20–24.Mar.1989; 1 ♂, Jan.1990; 1 ♂, 26–27.Jan.1990; 2 ♂, 1–3.Feb.1990; 2 ♂, 9–10.Feb.1990; 7 ♂, 12–15.Mar.1990; 1 ♂, 13–21.Mar.1990; 8 ♂, 15–18.Mar.1990; 2 ♂, 21–23.Mar.1990; 1 ♂, 25–26.Mar.1990; 2 ♂, 29–30.Mar.1990; 2 ♂, 1.Apr.1990; 1 ♂, 28–30.Nov.1990; 1 ♂, 7–9.Dec.1990; 1 ♂, 25.Dec.1990 (EMUS). **MEXICO:** JALISCO: Carayes, 17 ♂, 12.II. –19.Mar.1997, F.D. Parker coll. (EMUS); Chamela Research Station, 1 ♂, 6.Aug.1986, M. Sanchez coll. (EMUS).

Distribution.—Southern Mexico, Guatemala, and Costa Rica.

Remarks.—This is the first record of this species in Costa Rica. Additionally, the numerous specimens from Jalisco, Mexico suggest that the initial record from Nayarit, Mexico (Pitts and Manley 2004) is well within the range of this northern Neotropical species.

Lomachaeta hedera Williams & Pitts, new species

(Figs 1, 2)

Diagnosis.—This species can be separated from other male *Lomachaeta* species by the following combination of unique characters: the mandible is unarmed ventrally, T2 is black and lacks an apical fringe of thickened bristles, and the paramere has long setae ventrally in the apical half (Fig. 1).

Male holotype.—Coloration: Head, mesosoma, metasoma, and legs dark brown. Mandible reddish-brown, darkened basally and apically. Tegula brown. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T5-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front with deep dense punctures. Vertex with moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Clypeus densely punctate, rounded anteriorly. Antennal scrobe ecarinate. Gena weakly carinate. Ocelli minuscule; ocellocular distance 5X diameter of lateral ocellus, interocellar distance >3X lateral ocellar diameter. Flagellomere I 1.0X pedicel length; flagellomere II 1.7X pedicel length. *Mesosoma*: Pronotum with deep dense punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with sparse punctures. Mesopleuron with deep dense punctures. Metapleuron glabrous. Scutellum slightly convex with deep dense punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, with evenly rounded anterior and dorsal faces, punctures moderately spaced. T2 with deep moderately spaced punctures; S2 with deep, sparse punctures. T3-6 with small

moderately spaced punctures; S3-6 with small moderately spaced punctures. Pygidium with deep dense punctures. Hypopygidium with deep punctures, emarginate apically. *Genitalia* (Figs 1, 2): Paramere slightly laterally compressed, acuminate apically, and with long ventral setae along apical half. Penis valve unidentate apically.

Length.—4–5 mm.

Female.—Females collected at the same time and locality as the males are known, but we hesitate to describe them without additional evidence, because both *L. cirrhomeris* Pitts & Manley and *L. hicksi* Mickel have been collected in Baja California previously.

Host.—Unknown.

Type material.—***HOLOTYPE*: MEXICO:** BAJA CALIFORNIA SUR: Arroyo San Gregorio, 13 air km WNW La Purissima, ♂, 24–26.Apr.1983, M.S. Wasbauer coll. (CDFA). ***PARATYPES*: MEXICO:** BAJA CALIFORNIA SUR: Arroyo San Gregorio, 13 air km WNW La Purissima, 2 ♂, 24–26.Apr.1983, M.S. Wasbauer coll. (CDFA); Rancho Tablon, 13 km S Guillermo, 4 ♂, 16–18.Apr.1983, J. Slansky coll. (CDFA); Eastern edge of Sierra Placeres, 1 ♂, 24.Mar.1984, W.J. Pulawski coll. (CASC).

Distribution.—Baja California Sur, Mexico.

Etymology.—Named after JPP's daughter Ivy using the Latin name of the plant that is commonly called ivy (*Hedera*). Treat as a noun in apposition.

Remarks.—This species is morphologically similar to *L. ilex*, **sp. nov.**, and can be separated from that species by the setal pattern of the paramere (Figs 1, 3). Additionally, most specimens of *L. hedera* have black or dark brown tegulae, while all *L. ilex* specimens have orange or red tegulae. There is one specimen of *L. hedera*, however, with dark red tegulae, so the genitalia should also be used for identification.

The holotype and all of the paratypes were collected during March and April, suggesting that this species has spring seasonality.

Lomachaeta hyphantria Pitts & Manley, 2004

Lomachaeta hyphantria Pitts & Manley 2004: 11. Holotype male: Bolivia, Dep. Beni, Rio Itenez, 4 km above Costa Marque, Brazil, 12–18.Sep.1964, J.K. Bowseman and J. Lussenhop (AMNH).

Lomachaeta garm Williams & Pitts 2007: 299. Holotype male: **Colombia**, *Bolivar*, PNN Gorgona La Suiris, 2.Mar.2001-17.Mar.2001, coll. R Duque (IAvH). **Syn. nov.**

Diagnosis.—This species can be separated from all other *Lomachaeta* by the following combination of characters: the mandible is unarmed ventrally, the gena is carinate, the apical fringe of T2 has thickened brown bristles (e.g. Fig. 19), and the paramere is virtually asetose. *Genitalia*: See Pitts and Manley (2004: 12, 26) and Williams and Pitts (2007: 300, 326).

Length.—3–6 mm.

Female.—Unknown.

Host.—Unknown.

Material examined.—**BRAZIL:** RONDONIA: 62 km SE Ariquemas: 1 ♂, 22–31.Oct.1997, W.J. Hanson coll. (EMUS), 2 ♂, 1–14.Nov.1997, W.J. Hanson coll. (EMUS); Rio Guapore, opposite mouth of Rio Baures (Bolivia), 1 ♂, 26.Sep.1964, Bouseman & Lussenhop coll. (AMNH). **ECUADOR:** SUCUMBIOS: Rio Napo nr Sancha Lodge, 1 ♂, 12–22.May.1995, S. & J. Peck coll. (EMUS). **VENEZUELA:** ARAGUA: El Limon, 2 ♂, 26.Mar.1987, R. Miller & L.A. Stange coll. (FSCA).

Distribution.—Throughout northern South America: Colombia, Venezuela, Brazil, and Ecuador.

Remarks.—The holotype of this species has the integument of the head, mesosoma, and metasoma almost entirely dark brown. *Lomachaeta garm* Williams & Pitts was differentiated from *L. hyphantria* by differences in coloration, specifically in the orange head of *L. garm* (Williams and Pitts 2007). This was considered a valid distinction, because no intermediate color forms were recognized at the time, and the

specimens were widely separated geographically, with *L. garm* occurring in a lowland forest in northern Colombia, and *L. hyphantria* occurring in the southern Amazon Basin in Rondonia, Brazil and Beni, Bolivia.

Closer examination of specimens incorrectly identified as *Pseudomethoca* yielded additional South American *Lomachaeta*. These specimens were collected in rainforest habitats in Brazil, Ecuador, and Venezuela. In each of these specimens there is some level of orange integument on the head. One specimen from near Ariquemas, Brazil and the specimen from Ecuador have orange coloration restricted to a narrow ring around the eyes. The other two specimens from near Ariquemas, Brazil and the two specimens from Venezuela have more extensive orange coloration, with orange rings around the eyes and with the entire front orange as well. Discovery of new localities and these intermediate color forms is strong evidence that *L. garm* is simply a color variant of *L. hyphantria*. We, therefore, consider *L. garm* as a junior synonym of *L. hyphantria*.

This is one of the most widely distributed *Lomachaeta* species, potentially ranging throughout the northern forested regions of South America.

Lomachaeta ilex Williams & Pitts, new species

(Figs 3, 4)

Diagnosis.—This species can be separated from other male *Lomachaeta* species by the following unique combination of characters: the mandible is unarmed ventrally, the tegulae are red, T2 is black and lacks an apical fringe of thickened bristles, and the paramere has a long setae ventrally throughout its free length (Fig. 3).

Male holotype.—Coloration: Head and mesosoma black, metasoma and legs dark brown. Mandible orange, darkened basally and apically. Tegula pale orange. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T6-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front with deep dense punctures. Vertex with moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena ecarinate. Ocelli minuscule; ocellocular distance >5X length of lateral ocellus, interocellar distance 3X lateral ocellar length. Flagellomere I 0.9X pedicel length; flagellomere II 1.5X pedicel length. *Mesosoma*: Pronotum with dense punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with deep sparse punctures. Mesopleuron with dense punctures. Metapleuron glabrous. Scutellum slightly convex, with deep dense punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, with evenly rounded anterior and dorsal faces, punctures moderately spaced. T2 with deep sparse punctures; S2 with sparse punctures. T3-6 with small moderately spaced punctures; S3-6 with small moderately spaced punctures. Pygidium punctate, shagreened between punctures. Hypopygidium with deep punctures, emarginate apically. *Genitalia* (Figs 3, 4): Parameres slightly laterally flattened, acuminate apically, and with long ventral setae throughout free length of paramere. Penis valve unidentate apically.

Length.—4–5 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: USA:** NEVADA: South of Kaolin Wash, male, 22.May.1998, C. Schulz, K. Receveur, K. Keene, M. Andrus coll. (EMUS). ***PARATYPES*:** CALIFORNIA: *Imperial Co.*: Palo Verde, 1 ♂, 1.Apr.1968, R.M. Bohart coll. (UCDC); *San Bernardino Co.*: Cronise Valley, 1 ♂, 29.Apr.1956, M.S. Wasbauer coll. (CISC); Kelso Dunes Road, 1 ♂, 17–18.May.2003, D. Yanega coll. (UCRC); *San Diego Co.*: Borrego Valley: 4 ♂, 18.Apr.1957, R.M. Bohart coll. (UCDC, EMUS); 1 ♂, 18.Apr.1957, R.W. Bushing coll. (UCDC); 2 ♂, 19.Apr.1957, R.M. Bohart coll.

(UCDC); 1 ♂, 6.Apr.1964, F.D. Parker coll. (DGMC); NEVADA: *Clark Co.*: 4.5 mi SW Boulder, 2 ♂, 17.Sep.1997, Andrus, Griswold & Messinger coll. (EMUS); E of Logandale, 2 ♂, 20.May.1998, C. Schulz & K. Keen coll. (EMUS); Mormon Mesa, 1 ♂, 20.May.1998, C. Schulz, K. Receveur, K. Keene, M. Andrus coll. (EMUS); Toquop Wash, 1 mi N of Highway I-15, 1 ♂, 25.May.2003, G.R. Ballimer coll. (UCRC).

Distribution.—Mojave and western Sonoran Deserts in California and Nevada.

Etymology.—Named after JPP's daughter Holly using the Latin name of the plant that is commonly called holly (*Ilex*). Treat as a noun in apposition.

Remarks.—This species is morphologically similar to *L. hedera*, **sp. nov.**, and can be separated from that species by the setal pattern of the paramere (Figs 1, 3). All specimens of *L. ilex* have orange or red tegulae; while most specimens of *L. hedera* have black or dark brown tegulae. There is one specimen of *L. hedera*, however, with dark red tegulae, so the genitalia should be used for identification.

The holotype and all of the paratypes were collected during April, May, or September, suggesting that this species has spring and fall seasonality.

Lomachaeta litosisyra Williams & Pitts, new species

(Figs 5, 6)

Diagnosis.—This species can be separated from all other male *Lomachaeta* species by the shape of the paramere, which is cylindrical, down-curving apically, and has an apical tuft of long setae. The following characters are also useful for identification: the mandible is unarmed ventrally, T2 is black and lacks an apical fringe of thickened bristles, and the tegulae are red.

Male holotype.—Coloration: Head, mesosoma, and metasomal segments 1-6 black. Mandible dark orange, darkened basally and apically. Tegulae red. Legs brown, femora darkened. Tibial spurs white. Metasomal segment 7 orange-brown apically. Wings hyaline, veins brown. Ocellar area, mesonotum, and T4-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front deeply densely punctate. Vertex with deep, moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena ecarinate. Ocelli minuscule; ocellocular distance >6X length of lateral ocellus, interocellar distance >4X lateral ocellar length. Flagellomere I 0.9X pedicel length; flagellomere II 1.2X pedicel length. *Mesosoma*: Pronotum with moderately spaced punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with deep, moderately spaced punctures. Mesopleuron with deep dense punctures. Metapleuron glabrous. Scutellum slightly convex, with deep dense punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, with evenly rounded anterior and dorsal faces, punctures deep and dense. T2 with deep, moderately spaced punctures; S2 with deep, moderately spaced punctures. T3-6 with moderately spaced punctures; S3-6 with small dense punctures. Pygidium punctate. Hypopygidium punctate, emarginate apically. *Genitalia* (Figs 5, 6): Parameres elongate, cylindrical, down-curving apically, and with apical tuft of long setae. Penis valve unidentate apically.

Length.—4–6 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: USA:** ARIZONA: *Santa Cruz Co.*: 12 km E Arivaca, ♂, 3–7.May.2004, M.E. Irwin & F.D. Parker coll. (EMUS). ***PARATYPES*: MEXICO:** SONORA: San Carlos, 1 ♂, 3.Sep.1970, G.E. & R.M. Bohart coll. (EMUS). **USA:** ARIZONA: *Pima Co.*: Ina, Oracle, vic. Tucson, 1 ♂, 7.Sep.1987, W.L. Nutting coll. (UAIC); Silver Reef Wash, 4 km E VaivaVo Tat Monoii Mountains, 2 ♂, 1–7.May.2006, M.E. Irwin coll. (EMUS); Tucson, 1 ♂, 30.Jul.1979, F.G. Werner coll. (UAIC); Vail Mountain Creek Wash, 1 ♂, 18–25.Apr.2006,

M.E. Irwin coll. (EMUS); *Santa Cruz Co.*: 5 mi. W of Arivaca Junction, 1 ♂, 2.Apr.1986, T. Griswold coll. (EMUS).

Distribution.—Southern Arizona and northern Sonora, Mexico.

Etymology.—From the Greek *litos* "simple" and *sisyra* "garment", in reference to the dull gray setae covering the insect.

Remarks.—The apical tuft of setae on the paramere of this species is similar to that of *L. vacamuerte*, **sp. nov.** (Fig. 17), and where these species co-occur they share similar coloration, most notably, the tegulae are red. To identify this species, full extraction of the genitalia is often necessary in order to recognize the down-curved paramere shape, which is distinctive of *L. litosisyra*, **sp. nov.** (Fig. 5).

Lomachaeta megomicron Williams & Pitts, new species
(Figs 7, 8)

Diagnosis.—This species can be separated from all other *Lomachaeta* species by the following combination of characters: the mandible is unarmed ventrally, the gena is weakly carinate, the apical fringe of T2 has thickened brown bristles (e.g. Fig. 19), and the paramere has an apical tuft of setae (Fig. 7).

Male holotype.—Coloration: Head, mesosoma, metasomal segments 1-6 black, except apical band of T1 hyaline. Mandible orange, darkened basally and apically. Tegulae brown. Coxae and femora dark brown, tibiae and tarsi orange-brown. Tibial spurs white. Wings slightly infuscated, veins brown. Ocellar area, mesonotum, and T2 clothed with interspersed white, golden, and brown erect setae; remaining setae white. Fringes of T2-4 each having row of pale golden bristles in addition to simple setae. *Head*: Rounded posteriorly. Head contiguously punctate throughout, nearly reticulate. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena weakly carinate. Ocelli small; ocellocular distance 4X length of lateral ocellus, interocellar distance 1.8X lateral ocellar length. Flagellomere I equal to pedicel length; flagellomere II 1.2X pedicel length. *Mesosoma*: Pronotum with coarse contiguous punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with large, closely spaced punctures. Mesopleuron contiguously punctate. Metapleuron glabrous. Scutellum slightly convex with deep, dense punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 disciform, punctures moderately spaced. T2 with deep, dense punctures; S2 with deep, moderately spaced punctures. T3-6 with medium, dense punctures; S3-6 with small, dense punctures. Pygidium punctate. Hypopygidium with deep punctures, emarginate apically. *Genitalia* (Figs 7, 8): Parameres cylindrical, acuminate apically, and with apical tuft of setae. Penis valve unidentate apically.

Length.—4–6 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: ARGENTINA:** SALTA: 8 km N La Viña, ♂, 26.Oct.–13.Nov.2003, M.E. Irwin & F.D. Parker coll. (EMUS). ***PARATYPES*: ARGENTINA:** CATAMARCA: San Pablo, 6 ♂, 24.Oct.–12.Nov.2003, M.E. Irwin & F.D. Parker coll. (EMUS); SALTA: 8 km N La Viña, 3 ♂, 26.Oct.–13.Nov.2003, M.E. Irwin & F.D. Parker coll. (EMUS).

Distribution.—Argentina: Salta and Catamarca Provinces.

Etymology.—From the Greek *"mega"*, meaning large, and the fifteenth Greek letter *"Omicron"*, which resembles the Latin letter "O", in reference to the large, nearly circular eyes.

Remarks.—This male is likely conspecific with either *L. viani* Casal or *L. ibarrai* Casal, which both occur in Argentina and were described from females only (Casal 1969).

This species appears most closely related to *L. hyphantria*, the only other male species known from South America, because both species possess a genal carina, although the genal carina of *L. megomicron*, **sp. nov.**, is

much less developed than that of *L. hyphantria*.

Lomachaeta polemomechana Williams & Pitts, new species
(Figs 9, 10)

Diagnosis.—Lomachaeta polemomechana, **sp. nov.**, can be separated from other males by the following combination of characters: the mandible is unarmed ventrally, T2 lacks a row of thickened bristles, and the parameres are aciculate apically and lack long setae, instead only having setae that are shorter than the width of each paramere (Fig. 9).

Male holotype.—Coloration: Head, mesosoma, metasoma, and legs black. Mandible orange-brown, darkened basally and apically. Tegulae brown. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T5-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front deeply confluently punctate. Vertex with deep, moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena weakly carinate. Ocelli minuscule; ocellocular distance >5X length of lateral ocellus, interocellar distance 4X lateral ocellar length. Flagellomere I 1.0X pedicel length; flagellomere II 1.4X pedicel length. *Mesosoma*: Pronotum with deep dense punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with deep, sparse punctures. Mesopleuron with deep confluent punctures. Metapleuron glabrous. Scutellum slightly convex, with deep confluent punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 weakly disciform, with deep confluent punctures. T2 with deep, moderately spaced punctures; S2 with deep, moderately spaced punctures, slightly larger than those on T2. T3-6 with small sparse punctures; S3-6 with small sparse punctures. Pygidium punctate, granulate between punctures. Hypopygidium with deep punctures, emarginate apically. *Genitalia* (Figs 9, 10): Parameres slightly laterally flattened, acuminate apically, and clothed exclusively with short setae that are scattered throughout the free length. Penis valve unidentate apically.

Length.—4–6 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: MEXICO:** SONORA: 30 km E Agua Prieta, ♂, 19.Aug.2001, R.E. Minckley coll. (EMUS). ***PARATYPES*: USA:** ARIZONA: *Cochise Co.*: Paradise Rd., 3 mi. W Portal, 1 ♂, 26–28.Jul.2006, K.A. Williams & J.S. Wilson coll. (EMUS); *Pima Co.*: Baboquivari Mountains, Brown Canyon, 1 ♂, 16.Jun.2000, C.A. Olson & K. Will coll. (UAIC); *Santa Cruz Co.*: Ruby Mt., 20 km SSE Arivaca, 2 ♂, 3–7.May.2004, M.E. Irwin & F.D. Parker coll. (EMUS).

Distribution.—Southern Arizona and northern Sonora, Mexico.

Etymology.—From the Greek *polemikos* "warlike" and *mechanos* "machine".

Remarks.—The paramere of this species is similar to that of *L. chionothrix* Pitts & Manley, *L. cirrhomeris* Pitts & Manley, and *L. hicksi* Mickel, in that all of the setae are shorter than the paramere width. Each of those species has a well-developed ventral mandibular tooth, while *L. polemomechana*, **sp. nov.**, lacks a ventral tooth. Additionally, *L. cirrhomeris*, *L. chionothrix*, and *L. hicksi* each have thickened bristles at the apex of T2, while *L. polemomechana* has simple setae only on T2.

Lomachaeta powelli Mickel, 1964, new combination
(Figs 11, 12)

Smicromutilla powelli Mickel 1964: 108, 1 fig. male female, holotype male: USA, California, San Luis Obispo Co., 30.Apr.1962, J. Powell (CISC). **Comb. nov.**

Diagnosis of male.—This species can be separated from other male *Lomachaeta* by

the drastically reduced wing venation. The following characters are also useful for identification: the mandible is unarmed ventrally, the tegulae are orange or red, the integument of T2 is orange or red, the apical fringe of T2 lacks thickened bristles, and the paramere is virtually straight, aciculate apically, and lacks long setae.

Description of male genitalia (Figs 11, 12): Parameres slightly laterally flattened, acuminate apically, and clothed only with sparse, short setae. Penis valve unidentate apically.

Length.—3–6 mm.

Host.—The type specimens were collected crawling among a ground-nesting aggregation of *Diodontus occidentalis* Fox. This is an interesting, yet somewhat dubious, host record, in that all other *Lomachaeta* have been reared from twig- or mud-nesting crabronid wasps.

Material examined.—**USA:** CALIFORNIA: Sacramento Co.: Carmichael, 1 ♂, 16.Jun.1966, R.F. Wilkey coll. (UMSP).

Distribution.—Central Valley and Coast Range of California.

Remarks.—This is the type species of *Smicromutilla* Mickel. The genitalia of *L. powelli* (Mickel) have not been illustrated in the previous literature. The genitalic morphology is similar to that of other *Lomachaeta*, including the type species, *L. hicksi* Mickel.

Lomachaeta ptilohyalus Pitts & Manley, 2004

Lomachaeta ptilohyalus Pitts & Manley 2004: 12. Holotype male: Mexico, Oaxaca, 10 m North of Huajuapan de Leon, 7.Mar.1985, L. Stange & R. Miller (CNCI).

Diagnosis.—This species can be separated from all other *Lomachaeta* by the following combination of characters: the mandible is unarmed ventrally, the pronotum and mesonotum are sparsely punctate, the integument of metasomal segments 2 and 3 is red or orange, and the paramere is acuminate apically with long setae ventrally.

Genitalia: See Pitts and Manley (2004: 13, 26).

Length.—4–6 mm.

Female.—Unknown.

Host.—*Solierella plenoculoides similis.*

Material examined.—**USA:** ARIZONA: *Yuma Co.*: Yuma Proving Grounds, 1 ♂, 27.Jun.2001, S.L. Buchmann coll. (EMUS); Yuma Proving Grounds, site 531.3, 1 ♂, 26.May.2001, S.L. Buchmann coll. (EMUS).

Distribution.—Arizona and California in the United States and Oaxaca, Mexico.

Remarks.—The specimens from Arizona are identical to the previously recorded specimens of *L. ptilohyalus*, except that the apical setae of T2 are simple and pale yellow, rather than thickened orange bristles.

Lomachaeta snellingella Williams & Pitts, new species

(Figs 13, 14)

Diagnosis.—This species can be separated from all other *Lomachaeta* by the black metasomal integument and the shape of the parameres, which are dorsoventrally flattened and rounded apically (Fig. 13). Additionally, this species has the mandibles unarmed ventrally and lacks thickened bristles on the apex of T2.

Male holotype.—Coloration: Head, mesosoma, metasoma and legs dark brown. Mandible orange, darkened basally and apically. Tegula brown. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T6-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front with moderately spaced to dense punctures. Vertex with moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena ecarinate. Ocelli minuscule; ocellocular distance 5X length of lateral ocellus, interocellar distance >3X lateral ocellar length. Flagellomere I 1.0X pedicel length; flagellomere II 1.5X pedicel length. *Mesosoma*: Pronotum with moder-

ately spaced punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with moderately spaced punctures. Mesopleuron with moderately spaced punctures. Metapleuron glabrous. Scutellum slightly convex, with deep moderately spaced punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, with evenly rounded anterior and dorsal faces, punctures moderately spaced. T2 with shallow moderately spaced punctures; S2 with deep, moderately spaced punctures. T3-6 with sparse punctures; S3-6 with moderately spaced punctures. Pygidium punctate. Hypopygidium punctate, emarginate apically. *Genitalia* (Figs 13, 14): Parameres lamellate with apex evenly rounded, dorsoventrally flattened, down-curved apically, and with sparse, short setae along the internal and external surfaces. Penis valve unidentate apically.

Length.—3–5 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: USA:** CALIFORNIA: *San Diego Co.*: Borrego Valley, ♂, 19.Apr.1957, R.M. Bohart coll. (UCDC). ***PARATYPES*: USA:** CALIFORNIA: *Riverside Co.*: Deep Canyon Reserve, 3.5 km S Palm Desert, 1 ♂, 21.Apr.1973, K.L. Andrews coll. (UCRC); Thousand Palms: 1 ♂, 3.Apr.1955, W.R. Richards coll. (DGMC); 1 ♂, 11.Apr.1970, R.M. Bohart coll. (UCDC); Thousand Palms Canyon, 2 ♂, 8.Apr.1969, E. Grissel coll. (UCDC); *San Diego Co.*: Borrego, 1 ♂, 30.Apr.1957, F.X. Williams coll. (CASC).

Distribution.—Western Sonoran Desert in southern California.

Etymology.—We are proud to name this species after the late Dr. Roy Snelling, in honor of his outstanding research on aculeate Hymenoptera.

Remarks.—The genitalia are similar to those of *L. beadugrimi* (Pitts & Manley). These two species can be separated by the metasomal coloration, orange in *L. beadugrimi* and black to dark brown in *L. snellingella*. Because a similar range of coloration has been noted in widespread individual *Lomachaeta* species (e.g., *L. hicksi*), it is possible that *L. snellingella* may prove to be synonymous with *L. beadugrimi*. None of the recognized specimens of *L. beadugrimi* or *L. snellingella*, however, show any trace of intermediate coloration. Because of this, we choose to describe *L. snellingella* as a discrete species.

All known specimens of *L. snellingella* have been collected in April, suggesting spring seasonality.

Lomachaeta theresa Williams & Pitts, new species

(Figs 15, 16)

Diagnosis.—This species can be separated from all other *Lomachaeta* by the following combination of characters: the mandible is unarmed ventrally, the gena lacks a ventral carina, the metasoma is concolorous with the head and mesosoma, and the apical fringe of T2 has thickened brown bristles (e.g. Fig. 19). The paramere is also diagnostic, in having long ventrally directed setae on the external margin of the basal 0.75X of the free length.

Male holotype.—Coloration: Head, mesosoma, and metasoma black; apical fringes of T2-7 brown. Mandible orange, darkened basally and apically. Legs brown, femora darker than trochanters, tibiae and tarsi. Tegula brown. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T4-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front with deep confluent punctures. Vertex with moderately spaced punctures. Mandible tridentate apically, unarmed ventrally. Antennal scrobes ecarinate. Genae ecarinate. Ocelli small; ocellocular distance >4X length of lateral ocellus, interocellar distance >2X lateral ocellar length. Flagellomere I 0.9X pedicel length; flagellomere II 1.2X pedicel length. *Mesosoma*: Pronotum with deep moderately

spaced punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with sparse punctures. Mesopleuron reticulate. Metapleuron glabrous. Scutellum slightly convex, with deep punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, punctures moderately spaced. T2 with small moderately spaced punctures; S2 with deep, moderately spaced punctures. T3-6 with small moderately spaced punctures; S3-6 with dense punctures. Pygidium punctate. Hypopygidium with deep punctures, emarginate apically. *Genitalia* (Figs 15, 16): Parameres slightly laterally flattened, acuminate apically, with scattered long downward pointing setae on external margin in basal 0.75X free length of paramere. Penis valve unidentate apically.

Length.—5–6 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: MEXICO:** SONORA: 42 km ENE Alamos, Rancho Las Encinitas, ♂, 28–31.Jun.2007, M.E. Irwin coll. (EMUS). ***PARATYPES*: MEXICO:** SONORA: 43 km E Alamos, Rancho San Pablo, 1 ♂, 1–5.Jun.2007, M.E. Irwin coll. (EMUS); La Posa, 1 ♂, 1–5.Jun.2007, M.E. Irwin coll. (EMUS).

Distribution.—Currently known only from Sonora, Mexico.

Etymology.—Named in honor of JPP's wife Theresa Pitts-Singer. Treat as a noun in apposition.

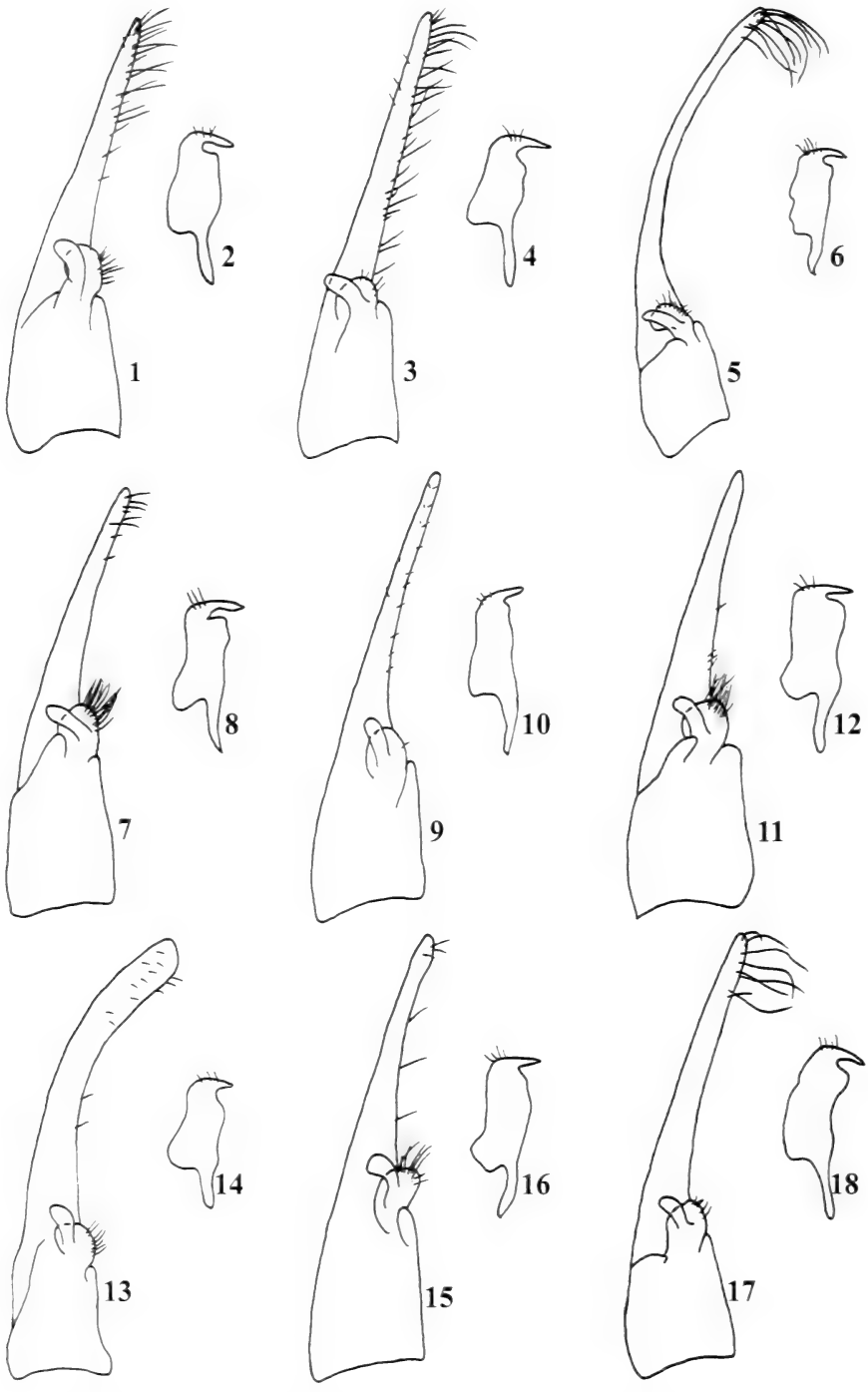
Remarks.—This species, *L. crocopinna* Manley & Pitts, and *L. ptilohyalus* Manley & Pitts are the only three North American *Lomachaeta* that have thickened bristles on the apex of T2, but lack a ventral mandibular tooth. *Lomachaeta theresa* can easily be separated from *L. crocopinna* and *L. ptilohyalus* by the black integument of T2 (T2 orange in *L. crocopinna* and *L. ptilohyalus*).

This species has the paramere more densely setose than the figure suggests, because the figure was drawn from the interal-lateral view (Fig. 15). There are numerous long setae along the external margin of the basal 0.75X of the paramere.

Lomachaeta vacamuerta Williams & Pitts, new species
(Figs 17, 18)

Diagnosis.—This species can be separated from all other *Lomachaeta* species by the following combination of characters: the mandible is unarmed ventrally, T2 is black and lacks an apical fringe of thickened bristles, and the paramere is virtually straight dorso-ventrally and has an apical tuft of long setae (Fig. 17).

Male holotype.—Coloration: Head, mesosoma, metasoma, and legs except tarsi black. Mandible black, orange-brown subapically. Tegula black. Tarsi brown. Tibial spurs white. Wings hyaline, veins brown. Ocellar area, mesonotum, and T4-7 clothed with interspersed white and brown erect setae; remaining setae white. *Head*: Rounded posteriorly. Front deeply confluently punctate. Vertex deeply densely punctate. Mandible tridentate apically, unarmed ventrally. Antennal scrobe ecarinate. Gena weakly carinate. Ocelli minuscule; ocellocular distance >5X length of lateral ocellus, interocellar distance 3X lateral ocellar length. Flagellomere I 1.0X pedicel length; flagellomere II 1.4X pedicel length. *Mesosoma*: Pronotum with deep dense punctures dorsally, glabrous with sparse punctures laterally. Tegula glabrous, except margin setigerously punctate. Mesonotum with deep sparse punctures. Mesopleuron with deep confluent punctures, metapleuron glabrous. Scutellum nearly flat, slightly convex, with deep, confluent punctures. Propodeum reticulate dorsally, glabrous laterally. *Metasoma*: T1 subsessile, with dense confluent punctures. T2 with deep, moderately spaced punctures; S2 with deep, moderately spaced punctures, slightly larger than those on T2. T3-6 with small moderately spaced punctures; S3-6 with dense punctures. Pygidium punctate. Hypopygidium punctate, emarginate



Figs 1–18. Male genitalia: lateral view, and penis valve. Figs 1–2: *Lomachaeta hedera*, **sp. nov.**; Figs 3–4: *L. ilex*, sp. **nov.**; Figs 5–6: *L. litosisyra*, **sp. nov.**; Figs 7–8: *L. megomicron*, **sp. nov.**; Figs 9–10: *L. polemomechana*, **sp. nov.**; Figs 11–12: *L. powelli*; Figs 13–14: *L. snellingella*, **sp. nov.**; Figs 15–16: *L. theresa*, **sp. nov.**; Figs 17–18: *L. vacamuerta*, sp. nov.

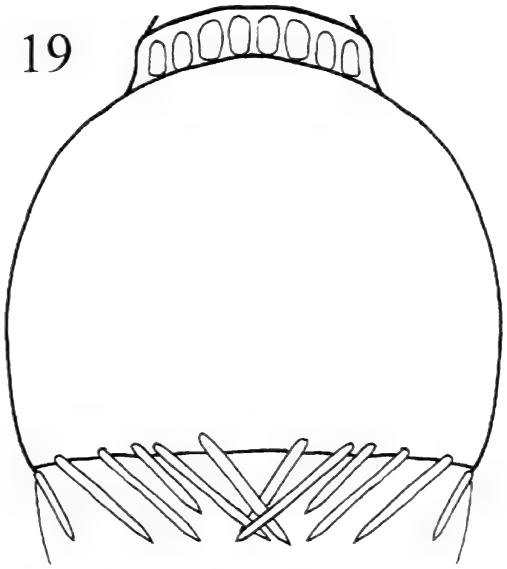


Fig. 19. Apical fringe of T2. Fig. 19: *Lomachaeta hicksi*, Mickel, reproduced from Pitts and Manley (2004) with permission from the authors.

apically. *Genitalia* (Figs 17, 18): Parameres cylindrical, weakly acuminate apically, with an apical tuft of long setae. Penis valve unidentate apically.

Length.—5–6 mm.

Female.—Unknown.

Host.—Unknown.

Type material.—***HOLOTYPE*: USA:** NEW MEXICO: *Chaves Co.*, Sagebrush Valley Road at Squaw Valley Road, ♂, 1–10.May.2004, M.E. Irwin coll. (EMUS); ***PARATYPES*: MEXICO:** SONORA: 28 km E Agua Prieta, 1 ♂, 22.Jun.2001, R.L. Minckley coll. (EMUS); 30 km E Agua Prieta, 1 ♂, 15.Apr.2001, R.L. Minckley coll. (EMUS). **USA:** ARIZONA: *Pima Co.*: Organ Pipe National Monument vic.: 3 ♂, 22.Apr.–2.May.2006, M.E. Irwin coll. (EMUS), 1 ♂, 2–12.May.2006, M.E. Irwin coll. (EMUS); Silver Reef Wash, 4 km E VaivaVo Tat Monoii Mountains, 17 ♂, 1–7.May.2006, M.E. Irwin coll. (EMUS); CALIFORNIA: *San Bernardino Co.*: Sheep Creek, 7.5 km NNE Wrightwood, 1 ♂, 25–30.May.2005, M.E. Irwin coll. (EMUS); NEW MEXICO: *Chaves Co.*, Sagebrush Valley Road at Squaw Valley Road, 15 ♂, 1–10.May.2004, M.E. Irwin coll. (EMUS); TEXAS: *Dimmit Co.*: 1.5 mi N Catarina, 1 ♂, 27.Apr.1985, W.J. Pulawski coll. (CASC); *Jeff Davis Co.*: Fort Davis, Point Rocks, 2 ♂, 30.May.1959, W.R.M. Mason coll. (CNCI); Davis Mountains Resort, 1 ♂, 16.May.–8.Jun.1998, D.G. Marqua coll. (LACM); *Kimble Co.*: Junction, 3 ♂, 6.May.1986, W.J. Pulawski coll. (CASC).

Distribution.—Arizona to Texas and Sonora, Mexico.

Etymology.—From the Spanish *vaca* "cow" and *muerte* "dead" in reference to a mistranslation of Cow Killer, an American common name for Mutillidae, and named in honor of Edmund E. Williams.

Remarks.—This is one of the most widely distributed *Lomachaeta* species, being found in all three hot Nearctic deserts (Chihuahuan, Mojave, and Sonoran) and in the mountainous Madrean Archipelago of southeastern Arizona. There is variation in coloration of the tegulae in this species; specimens from New Mexico and Texas have dark brown or black tegulae, while those from Arizona, California, and Sonora have reddish tegulae.

KEY TO MALES OF *LOMACHAETA*

1. Mandible having deep ventral excision with large ventral tooth (as in Pitts et al., 2009: Fig. 46) . . . . . 2 (*L. hicksi* species-group).
   Mandible weakly excised ventrally, lacking tooth . . . . 4 (*L. crocopinna* species-group).
2. Femora and tegulae orange brown or yellow brown, not concolorous with mesosoma . . . . . ***L. cirrhomeris* Pitts & Manley**
   Legs and tegulae black or dark brown, concolorous with mesosoma . . . . . 3.
3. Penis valve with one ventral tooth (see Pitts and Manley 2004: 26, Figs 16–18); mesonotal punctures sparsely spaced; integument of T2 often red or orange, at least laterally (Widespread in the Nearctic Region) . . . . . ***L. hicksi* Mickel**

Penis valve with two ventral teeth (see Pitts and Manley 2004: 26, fig. 14); mesonotal punctures closely spaced; integument entirely black (Costa Rica, Guatemala, and southern Mexico) ..... ***L. chionothrix* Pitts & Manley**

4. Metasoma orange to red, at least in part ..... 5.
Metasoma dark brown to black, concolorous with mesosoma ..... 8.

5. Paramere broadly flattened, rounded apically (as in Fig. 13) ..... ***L. beadugrimi* (Pitts & Manley)**
Paramere cylindrical, acuminate apically (e.g. Fig. 11) ..... 6.

6. Wing venation greatly reduced; paramere lacking long setae (Fig. 11) ... *L. powelli* (Mickel)
Wing venation normal; paramere having elongate setae ventrally (as in Fig. 3) ..... 7.

7. Punctures on pronotum and mesonotum more than 2 diameters apart; only metasomal segments 2 and 3 orange, sometimes middle of third tergite black brown (Arizona, California, and Mexico) ..... ***L. ptilohyalus* Pitts & Manley**
Punctures on pronotum and mesonotum less than 2 diameters apart; metasoma orange, except metasomal sternum 1 black brown (southwestern United States) ..... ***L. crocopinna* Pitts & Manley**

8. Apical fringe of T2 having thickened bristles apically (e.g. Fig. 19) ..... 9.
Apical fringe of T2 having simple setae only ..... 11.

9. Vertex having moderately spaced punctures; paramere having long setae on external surface of basal 0.75X of free length (Sonora, Mexico) ..... ***L. theresa* sp. nov.**
Front and vertex contiguously punctate, verging on reticulate, sometimes indistinct; paramere lacking long setae basally (South America) ..... 10.

10. Gena weakly carinate; apex of paramere having weak tuft of long setae (Argentina; Fig. 7) ..... ***L. megomicron* sp.nov.**
Genal carina well-defined, distinct; paramere lacking apical tuft (northern South America; as in Fig. 9) ..... ***L. hyphantria* Pitts & Manley**

11. Parameres flattened, rounded apically (Fig. 13) ..... ***L. snellingella* sp. nov.**
Parameres cylindrical or aciculate (Figs 1, 3, 5, 9, 17) ..... 12.

12. Paramere lacking long setae, all setae shorter than paramere width (Fig. 9) ..... ***L. polemomechana* sp. nov.**
Paramere having long setae ventrally, some setae longer than paramere width (Figs 1, 3) ..... 13.

13. Long ventral setae present throughout length of paramere (Fig. 3) (Mojave & Western Sonoran Deserts) ..... ***L. ilex* sp. nov.**
Paramere lacking long setae basally, either having apical tuft of setae (Figs 5, 17) or having long setae ranging through apical half of paramere (Fig. 1) ..... 14.

14. Paramere curving ventrally (Fig. 5) ..... ***L. litosisyra* sp. nov.**
Paramere virtually straight (Figs 1, 17) ..... 15.

15. Long setae of paramere restricted to tuft in apical fifth of free length (Fig. 17) ..... ***L. vacamuerte* sp. nov.**
Long setae of paramere scattered throughout apical half of free length (Fig. 1) ..... ***L. hedera* sp. nov.**

ACKNOWLEDGMENTS

We thank Juanita Rodriguez-Arrieta, Joseph S. Wilson, and Carol D. von Dohlen for advice and assistance with the manuscript. We are grateful to all of the collection managers and curators for loan of necessary material, especially Robert Zuparko (CISC, CASC), Steve Gaimari (CDFA), and Lynn Kimsey (UCDC). We also thank Frank Parker and Mike Irwin for their outstanding prowess with Malaise trapping techniques. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, UT and was approved as journal paper no. 8079.

LITERATURE CITED

Casal, O. H. 1969. Sobre *Lomachaeta* Mickel, 1936 (Hymenoptera, Mutillidae). *Physis, Revista de la Sociedad Argentina de Ciencias Naturales* 29: 33–35.

Mickel, C. E. 1936. Two new genera and five new species of Mutillidae. *Annals of the Entomological Society of America* 29: 289–297.

———. 1940. Two new species of *Lomachaeta*, with a key to described species. *Pan-Pacific Entomologist* 16: 127–131.

———. 1964. A new genus and species of Mutillidae from California. *Pan-Pacific Entomologist* 40: 108–110.

Pitts, J. P. and D. G. Manley. 2004. Review of *Lomachaeta* Mickel (Hymenoptera: Mutillidae) of North and Central America. *Zootaxa* 474: 1–27.

———, J. S. Wilson, K. A. Williams, and N. F. Boehme. 2009. Velvet Ants (Hymenoptera: Mutillidae) of the Algodones Sand Dunes of California, USA. *Zootaxa* 2131: 1–53.

Quintero, D. and R. A. Cambra. 1996. Contribución a la sistemática de las mutilidas (Hymenoptera) del Perú, en especial las de la Estación Biológica BIOLAT, Río Manu, Pakitza. Pp. 327–357 *in* Wilson, D. E. and A. Sandoval, eds. *Manu: The Biodiversity of Southeastern Peru*. Washington DC, Smithsonian Institution Press, 679 pp.

Williams, K. A. and J. P. Pitts. 2007. New species of the predominately temperate velvet ant genera *Lomachaeta* Mickel and *Sphaeropthalma* Blake from Central and northern South America (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 133: 297–326.

J. HYM. RES.
Vol. 18(2), 2009, pp. 244–281

The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part III. New and Little Known Species with Incomplete Venation

FRIEDRICH W. GESS

Albany Museum, Grahamstown, 6140 South Africa; email: F.Gess@ru.ac.za

Abstract.—In this publication, the third of a projected series revising the Afrotropical (essentially southern African) species of the genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae), seventeen species are dealt with. Twelve **new species** from Namibia are described. They are: ***bella***, ***clypeata***, ***codoni***, ***maculipennis***, ***mandibulata***, ***parva***, ***pteroniae***, ***pulawskii***, ***setosa***, ***tuberculifera***, ***tuberculiventris*** and ***tuberculiventroides***.

With regard to five known species, *albopicta* (Richards), *diana* (Richards), *minima* Schulthess, *poecila* Schulthess and *propinqua* Schulthess, the descriptions of *albopicta* and *diana* are augmented by those of the hitherto unknown males, the descriptions of *minima* and *poecila* are corrected with reference to the type material and are augmented, in the case of *minima*, by an account of intra specific variation shown by a large sample from the seaboard of the Namib north of Swakopmund and, in the case of *poecila*, by an account of a remarkable geographic cline in colour pattern shown by specimens collected from localities ranging from Swakopmund (the type locality) in the north to Hondeklip Bay in the south.

Extensive collecting data pertaining to all seventeen species contribute to the knowledge of their distribution and floral associations.

An addendum to species described by Gess (2007) gives additional collecting data for *Q. bonaespei*, *Q. conchicola* and *Q. vexillata*.

I am very pleased to have the opportunity to record in this Festschrift my appreciation and gratitude to Roy Snelling for his generosity in 2001 when, in his personal capacity, he contributed towards the cost of replacing the deficient cabinets which up to that time housed the Hymenoptera collection of the Entomology Department of the Albany Museum.

The background to the present state of knowledge of the taxonomy of the genus *Quartinia* Ed. André, 1884 has been fully stated in Gess (2007).

Desirable as it might be to undertake a complete revision of the genus, this is at present not practicable. Rather than to get bogged down in a study which might never be completed and published, it is intended to publish a series of papers describing new species as well as reviewing some known species. It is envisioned that a new key to species will complete the series. To date Parts I and II have been published as Gess (2007) and Gess (2008) respectively.

Quartinia species range in length from a little over 2 mm to 7 mm. In comparison with the great majority of species of other genera of Masarinae even the largest *Quartinia* are relatively small. In view of the considerable range in size shown by species of *Quartinia* and in order to express relative size, categories based on length have been established for species of the genus. These are: minute (1.5–2.5 mm); small (2.5–3.5 mm); medium (3.5–4.5 mm); large (4.5–5.5 mm); very large (5.5–6.5 mm); and gigantic (6.5–7.5 mm).

The present paper deals with species with incomplete venation (2*m-cu* present

but attenuate and interrupted)–that is species which in the past would have been placed in *Quartinioides* Richards, 1962 but synonymized with *Quartinia* Ed. André by van der Vecht and Carpenter (1990).

While the present paper was in preparation I received a request from Ms. Candice Lyons, a Masters student of the University of Cape Town, to help with the determination of a large number (over 1100) of specimens of various species of *Quartinia* derived from her study of the measure of success of restoration techniques on two strip-mining sites on the Namaqualand coast–one a De Beers mine in the Northern Cape and the other the Namaqua Diamond Company mine in the Western Cape. In return for the determinations Ms. Lyons kindly agreed to house her voucher material in the Albany Museum and to allow me to use it and the associated data for my own purposes. In doing so, I have reduced the co-ordinates, as given by her, to the nearest minute in keeping with the way in which co-ordinates are given by myself. In the present paper additional data derived from this material will be found under *Q. poecila* and in the addendum to species described by Gess (2007) under *Q. conchicola* and *Q. vexillata*.

In the addendum also is given the collecting data of an additional specimen of *Q. bonaespei* collected by myself in 1960 and found amongst material on loan from the South African Museum.

Acronyms for institutions in which material is housed are: AMG = Albany Museum, Grahamstown, South Africa; AMNH = American Museum of Natural History, New York, United States of America; BMNH = Natural History Museum, London, England; CAS = California Academy of Sciences, San Francisco, United States of America; FSCA = Florida State Collection of Arthropods, Gainesville, United States of America; NCP = National Collection of Insects, Pretoria, South Africa; NNIC = Namibian National Insect Collection, Windhoek, Namibia; SAM = South African Museum, Iziko Museums of Cape Town, South Africa.

DESCRIPTION OF SPECIES AND COLLECTION DATA

Quartinia albopicta (Richards)

Quartinioides albopicta Richards, 1982: 199, ♀. Holotype: ♀, Namibia: Gobabeb (Zoological Museum, Copenhagen).

Diagnosis.—Small (2.5–3.5 mm long). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula with posterior inner corner inwardly produced, yellow (except for pale testaceous discal spot). Both sexes with head and thorax extensively yellow marked, gaster predominantly yellow. Head with following yellow: entire clypeus; broad band from bottom of one ocular sinus to the other, medially broadly connected to the clypeus; occipital band from gena to gena, extending down almost to malar space. Mesoscutum with four longitudinal yellow streaks, namely medial pair (broadly fused basally) and lateral pair flanking tegulae; medial and lateral streak of each side anteriorly produced and meeting in a smoothly rounded loop on anterior third of mesoscutum.

Description.—Female (additional to Richards' description): Head 1.28 × as wide as long (average of 5; range 1.26–1.31). Clypeus 1.32 × as wide as long (average of 5; range 1.28–1.34).

Male (hitherto undescribed): Very similar in coloration and colour pattern to female, most noticeably differing in: the more abruptly set off darker distal half of the antennal club; the almost complete replacement by yellow of the black area surrounding the antennal socket (that is on the frons above the socket, on the side of the clypeus and on the paraocular area); the yellow base of the mandible; the lighter colour of the sterna. Length 2.5–2.9 mm; length of fore wing 1.7–1.9 mm; hamuli 4.

Head 1.37 × as wide as long (average of 3; range 1.34–1.40). Clypeus 1.44 × as wide as long (average of 3; range 1.38–1.50); clypeal dorsal margin attaining level of a line joining the dorsal margins of the antennal sockets; distal margin deeply emarginate and widely lamellate (especially distolaterally) and with pigmented part distomedially very slightly raised and protruding into lamella; disk with sides rising steeply from paraocular area, distolaterally with long, inwardly curved, conspicuous setae. Labrum with a pronounced median carina, conspicuously and densely setose (especially immediately flanking carina); distal margin medially subangular.

Tergum VII with a shallow V-shaped apical incision, the lobes defining it rounded; apical margin of sterna VII + VIII with a narrow black median projection; parameres flattened, wide, distally with outer margin smoothly rounded to apex and inner margin with an emargination producing a proximal tooth and an apical hook.

Material examined.—NAMIBIA: Kuiseb River Delta near Rooibank (23.12S 14.39E), 18.iii.1983 (Nat. Coll. Kuiseb Survey), 21 ♀♀, 10 ♂♂ (all visiting flowers of *Trianthema hereroensis* Schinz, Aizoaceae: non-Mesembryanthema) [NCP]; Walvis Bay, 22.ii.1990 (W. J. Pulawski), 1 ♀, 12 ♂♂ [CAS]; Half Shaft Camp (23.41S 14.04E) [locality not traced; co-ordinates place it in the Atlantic], 1–7.iv.1986 (E. Griffin), 1 ♂ (Pres. pitfall traps) [NNIC]; 11 km S of Swakopmund on inland side of road B2 to Walvis Bay (22.46S 14.32E), 7.iv.2002, 60 ♀♀, 12 ♂♂; same locality, 14.iv.2002, 18 ♀♀, 1♂; same locality, 20.iv.2002, 27 ♀♀, 14 ♂♂; same locality, 30.iii.2004, 74 ♀♀, 13 ♂♂ (all F. W. and S. K. Gess) (all visiting pink flowers of *Trianthema hereroensis* Schinz, Aizoaceae: non-Mesembryanthema) [AMG].

Provenance of specimens examined by Richards (1962).—NAMIBIA: Gobabeb (25.36 S 15.10E) on downs.

Geographic distribution.—Known only from Namibia, from the vicinity of the Kuiseb drainage system which forms the northern limit of the Southern Namib of Giess (1971).

Floral associations.—Known only in association with *Trianthema hereroensis* Schinz (Aizoaceae: non-Mesembryanthema).

Nesting.—Unknown; possibly in the sand hummocks formed beneath the *Trianthema* plants.

Discussion.—Richards (1981) in comparing the structure of *Q. albopicta* with that of *Q. minima* von Schulthess correctly states that the head in front view is rather wider. However, his statement that the clypeus [of *albipicta*] is rather wider compared with its height [than is that of *minima*] is incorrect, the opposite being true. The error can be explained if comparison is made not with the holotype of *minima* but with the incorrect proportions for both head and clypeus given by Richards (1962) in his redescription of that species. [See also under *Q. minima* in the present publication.]

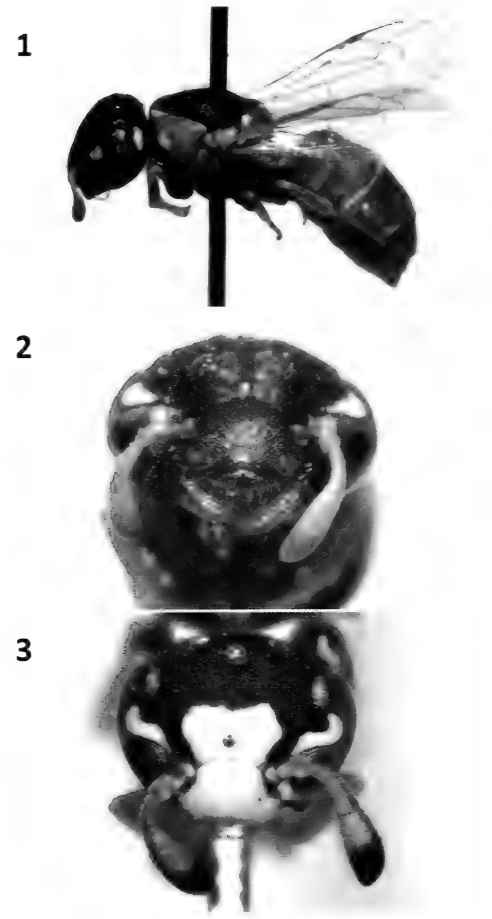
At the site 11 km S of Swakopmund on inland side of road to Walvis Bay (22.46S 14.32E) *Q. albopicta* was on all occasions found together with the much larger *Q. femorata* Gess, likewise visiting the flowers of *T. hereroensis* (see Gess 2007).

Quartinia bella Gess, new species
(Figs 1–3)

Quartinia sp. N5, Gess and Gess, 2003: 68 (flower visiting).

Diagnosis.—Small to medium sized (3.3–3.6 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins, and with 2*m-cu* interrupted before reaching M. Tegula with posterior inner corner inwardly produced. Both sexes black, reddish-brown (in many but not all specimens) and yellowish-white. Male with labrum carinate, tergum VII laterally distinctly angulate and apically usually with a narrow V-shaped incision, and sternum I postero-medially raised and produced into a small conical tubercle.

Description.—Female (Figs 1, 2): Black. The following are yellowish-white: under-



Figs 1–3. *Quartinia bella*: 1, ♀, dorso-lateral view (× 12); 2, ♀, head, front view (× 26); 3, ♂, head, front view (× 26).

side of antenna; two small supra-clypeal spots [in one specimen only]; small crescent at bottom of ocular sinus; small streak on temple behind upper part of eye; hind margin of pronotum (to postero-dorsal angle) and spot on humeral angle of same; small spot at top of mesopleuron; anterior and posterior parts of tegula; spot postero-medially on disk of scutellum; scutellar lamella; propodeal angles; narrow posterior bands (slightly expanded medially but not quite reaching sides) on terga I–VI; apex of femur and base of tibia of fore leg. Reddish-brown are: mandible; upperside of antenna; in some specimens most of pronotum other than for yellowish-white markings [in other specimens ground colour mostly black or black throughout]; diffuse area on upper part of mesopleuron; median region of tegula; in some specimens diffuse spot on each side of scutellar disk [in other specimens ground colour black]; entire propodeum [in one specimen only]; entire gaster other than for yellowish-white bands; most of tibia and tarsus of all legs. Wings very lightly browned; veins brown.

Length 3.3–3.6 mm (average of three specimens: 3.47 mm): length of fore wing 2–2.4 mm (average of three: 2.16 mm); hamuli 4–5.

Head in front view 1.2 × as wide as long (average of three specimens); finely microreticulate (shagreened), moderately shiny; frons and vertex with small, indistinct, shallow punctures separated by their width or more. POL: OOL = 1: 0.8. Clypeus 1.6 × as wide as long; anterior margin shallowly and widely emarginate; antero-lateral angles rounded.

Mesosoma microreticulate, moderately shiny, with punctures, particularly on mesonotum, slightly larger but much more distinct than on frons.

Gaster shiny, not obviously microreticulate or punctured.

Male (Fig. 3): Black. The following are yellowish-white: mandible; underside of antenna (except last two flagellomeres); labrum; clypeus; large marking on lower half of frons (contiguous with yellowish-white clypeus) either roughly transversely oval and centrally including a small dark brown spot or [in a minority of specimens] broadly U- shaped; paraocular region below antennal insertion and dorsally widening streak in ocular sinus [in some specimens these two pale areas narrowly connected]; large streak on temple behind upper part of eye; hind margin of pronotum (to postero-dorsal angle) and spot on humeral angle of same; small spot at top of mesopleuron; anterior and posterior parts of tegula; spot postero-medially on disk of scutellum; scutellar lamella; propodeal

angles; narrow posterior bands (slightly expanded medially but not quite reaching sides) on terga I–VI. Reddish-brown are: upper side of scape, pedicel and proximal flagellomeres; in some specimens most of pronotum other than for yellowish-white markings [in other specimens ground colour black]; median region of tegula; in some specimens most of scutellar disk other than for postero-medial yellowish-white spot and ill defined light brown spot on each side [in other specimens ground colour black and lateral spot absent]; in same specimens entire gaster other than for yellowish-white bands [in other specimens declivous face of tergum I only; in others again ground colour black throughout].

Length 3.3–3.4 mm (average of 3: 3.37); length of fore wing 2.1–2.2 mm (average of 3: 2.17 mm); hamuli 5.

Head in front view 1.33 × as wide as long (2 specimens).

Clypeus 1.64× as wide as long (2 specimens); clypeal dorsal margin attaining a level only slightly exceeding an imaginary line joining dorsal margins of antennnal sockets; distal margin widely and shallowly emarginate, narrowly lamellate. Labrum with a median carina.

Tergum VII with hind margin smooth and narrowly lamellate, laterally distinctly angulate and apically with a narrow V-shaped incision [incision in specimen from 20 km S of Omaruru reduced to a small notch and in that from 26 km W of Kamanjab totally lacking]. Sternum I postero-medially raised and produced into a small conical tubercle.

Etymology.—The name *bella*, a Latin adjective meaning pretty, is intended to draw attention to the attractive appearance of the species.

Material examined.—Holotype: ♂, NAMIBIA: between Gaub and Kuiseb passes (23.27S 15.46E), 13.iii.2000 (F. W. and S. K. Gess) (visiting yellow flowers of *Adenolobus pechuelii* (Kuntze) Torre and Hillc., Fabaceae, Caesalpinoideae) [AMG]. Paratypes: NAMIBIA: 26 km W of Kamanjab (19.36S 14.28E), 7.iv.1998, 1 ♂ (visiting purple flowers of *Aptosimum angustifolium* Weber and Schinz, Scrophulariaceae); 120 km from Khorixas on road to Palm (20.17S 14.05E), 8.iv.1998, 19 ♀♀, 2 ♂♂ (13 ♀♀, 2 ♂♂ visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae; 4 ♀♀ visiting white flowers of *Boerhavia deserticola* Codd, Nyctaginaceae; 2 ♀♀ visiting pink flowers of *Gisekia africana* (Lour.) Kuntze, Moluginaceae); 20 km S of Omaruru by road to Karibib (21.35S 15.59E), 24.iii.1997, 1 ♀, 1 ♂ (visiting purple flowers of *Aptosimum arenarium* Engl., Scrophulariaceae); 12 km SW of Usakos (21.59S 19.29E), 23.iii.1997, 1 ♀ (visiting purple flowers of *Aptosimum arenarium*); 34 km SW of Usakos (22.02S 15.17E), 22.iii.1997, 11 ♀♀ (5 ♀♀ visiting yellow flowers of *Zygophyllum simplex*; 6 ♀♀ visiting purplish pink flowers of *Sesuvium* cf. *hydaspicum* (Edgw.) Gonc., Aizoaceae: non-Mesembryanthema); 117 km from Swakopmund on road to Usakos (22.02S 15.17E) [this is the same locality as the previous one], 16.iii.2000, 9 ♀♀ (visiting pink flowers of *Sesuvium* cf. *hydaspicum*); between Kuiseb and Gaub passes (23.20S 15.52E), 20.iii.2000, 3 ♀♀, 1 ♂ (visiting yellow flowers of *Tripteris microcarpa* (Harv.) T. Norl., Asteraceae); between Kuiseb and Gaub passes (23.24S 15.50E), 22.iii.1999, 5 ♀♀ (visiting white flowers of *Zygophyllum cylindrifolium* Schinz, Zygophyllaceae); between Kuiseb and Gaub passes (23.27S 15.46E), 22.iii.1999, 5 ♀♀ (3 ♀♀ visiting yellow flowers of *Zygophyllum simplex*; 2 ♀♀ visiting white flowers of *Zygophyllum cylindrifolium*); between Gaub and Kuiseb passes (23.27S 15.46E) [this is the same locality as the previous one], 13.iii.2000, 36 ♀♀, 36 ♂♂ (30 ♀♀, 32 ♂♂ visiting yellow flowers of *Adenolobus pechuelii* (Kuntze) Torre and Hillc., Fabaceae, Caesalpinoideae; 5 ♀♀, 1 ♂ visiting pink flowers of *Indigofera auricoma* E. Mey., Fabaceae, Papilionoideae; 1 ♀, 3 ♂♂ visiting purple/violet flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae)–(all F. W. and S. K. Gess) [all AMG]; Namib National Park, Homeb [locality not traced], 23.i.1988 (R. Miller and L. Stange) 10 ♀♀ [FSCA].

Geographic distribution.—Known from Namibia from localities spanning four degrees of latitude and falling in the Mopane Savanna, Thornbush Savanna, Semi Desert and Savanna Transition (Escarpment Zone) and Central Namib of Giess (1971).

Floral associations.—Recorded from seven plant families: Aizoaceae: non-Mesembryanthema (*Sesuvium*); Asteraceae (*Tripteris*); Fabaceae, Caesalpinoideae (*Adenolobus*); Fabaceae, Papilionoideae (*Indigofera*); Moluginaceae (*Gisekia*); Nyctaginaceae (*Boerhavia*); Scrophulariaceae (*Aptosimum*); Zygophyllaceae (*Zygophyllum*).

Nesting.—Unknown.

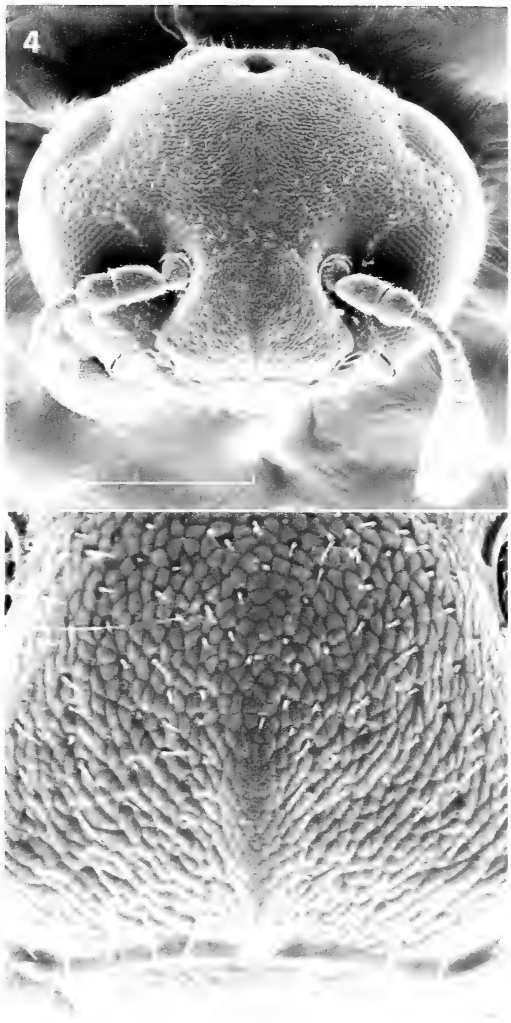
Discussion.—The species in both sexes shows considerable variation in colour pattern within a sample of a single population. This is a consequence of varying degrees of melanism in which the reddish-brown ground colour is partially or wholly replaced by black. This affects the colour pattern of the pronotum, scutellum and, in the males, the gaster. Variable also in the males is the shape of the supra-clypeal marking as indicated in the description.

With regard to morphology, the male shows considerable variation in the state of the apex of tergum VII: with a narrow V-shaped incision (the condition in the majority of the specimens examined); with the incision reduced to a small notch; without either incision or notch.

Quartinia clypeata Gess, new species (Figs 4, 5)

Quartinia sp. N6 Gess and Gess, 2003: 68 (flower visiting)

Diagnosis.—Small (2.6–3.5 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins and with 2*m-cu* interrupted before reaching M. Tegula with posterior inner corner rounded, not inwardly produced. Female with head, other than for narrow yellowish-white streak on temple, completely black (notably lacking pale marking in ocular sinus); male likewise but clypeus in some specimens asymmetrically marked by a number of small spots or by a single larger one. Male with distinct, rounded, median carina on lower half of clypeus (Figs 4, 5).



Figs 4, 5. *Quartinia clypeata*: 4, ♂, head, front view; 5, ♂, portion of clypeus showing median carina.

Description.—Female: Black. The following are yellowish-white: underside of flagellomeres (except ultimate); narrow streak on temple behind upper part of eye; medially interrupted band on anterior margin of pronotum and postero-dorsal angle of same (these markings in some specimens narrowly connected); in some specimens small spot on humeral angle; in some specimens narrow streak anteriorly on mesopleuron; tegula anteriorly and posteriorly (median part dark brown); median spot posteriorly on disk of scutellum and medially interrupted band on

lamellate margin of same; in some specimens propodeal angle; posterior bands, reaching sides, on terga I–IV or V; apex of femur and dorsal streak on tibia (or in some specimens almost entire tibia and tarsomeres) of all legs. Various shades of reddish-brown are: mandible; upper surface of antenna; in some specimens clypeus distally and clypeal lamella; in some specimens gaster partially (especially sides of terga, entire sterna).

Length 3.2–3.5 mm (average of 3: 3.3 mm); length of fore wing 2.2 mm; hamuli 4.

Head in front view 1.2 × as wide as long. POL: OOL = 1: 0.64. Clypeus, frons and vertex microreticulate (shagreened) without discernable punctures; mesonotum microreticulate and with small punctures (interstices equal to or exceeding puncture width).

Male (Figs 4, 5): In coloration and markings very similar to female. Most males, like all females, with head, other than for narrow yellowish-white streak on temple, completely black; a few males with clypeus asymmetrically marked by a number of small spots or by a single larger one. Labrum pale. Tergum VI with yellowish-white posterior band; tergum VII reddish-brown with area around apical incision paler. Surface sculpture as in female.

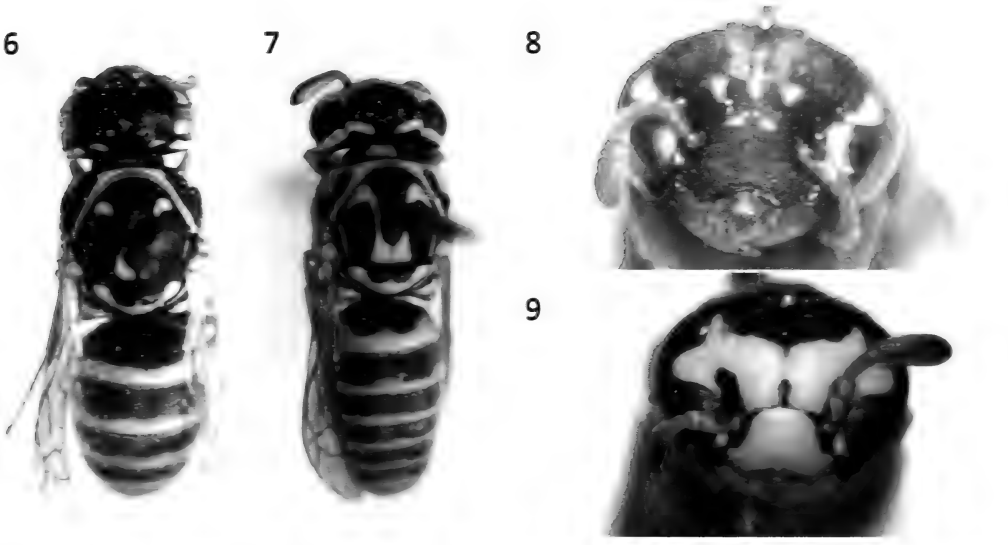
Length 2.6–3.0mm (average of 3: 2.87). fore wing 1.8 mm.

Head in front view 1.32 × as wide as long. Clypeus 1.36 × as wide as long; clypeal dorsal margin attaining a level only slightly exceeding an imaginary line joining dorsal margins of antennal sockets; distal margin narrowly lamellate, widely and shallowly emarginate and laterally smoothly rounded; clypeal disk convexly raised, with a distinct, rounded, median carina on lower half (Figs 4, 5). Labrum with a poorly developed, rounded, median carina.

Tergum VII with short V-shaped excision and rounded lateral lobes. Sterna unmodified.

Etymology.—The name *clypeata* serves to draw attention to the uniquely modified clypeus of the male.

Material examined.—Holotype: ♂, SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess) (visiting pale white-pink flowers of *Prenia sladeniana* (L. Bol.) L. Bol., Aizoaceae: Mesembryanthema) [AMG]. Paratypes: NAMIBIA: E of Oranjemund, 37 km from checkpoint on road to Sendelingsdrif (28.23S 16.44E), 24.ix. 1997, 7 ♀♀, 1 ♂ (3 ♀♀, 1 ♂ visiting yellow flowers of *Tripteris* sp., Asteraceae; 2 ♀♀ visiting white flowers of *Juttadinteria elizae* (Dinter and A. Berger) L. Bolus, Aizoaceae: Mesembryanthema; 2 ♀♀ visiting purple/violet flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae); E of Oranjemund, 34 km from checkpoint on road to Sendelingsdrif (28.24S 16.44E), 25 and 26.ix. 1997, 28 ♀♀, 6 ♂♂ (15 ♀♀, 6 ♂♂ visiting cream flowers of *Sarcocaulon* sp., Geraniaceae; 3 ♀♀ visiting yellow flowers of *Tripteris* sp.; 7 ♀♀ visiting white flowers of *Pteronia glabrata* L. f., Asteraceae; 3 ♀♀ visiting white flowers of *Brownanthus pubescens* (N. E. Br. ex C. A. Maas) Bullock, Aizoaceae: Mesembryanthema)–(all F. W. and S. K. Gess) [all AMG]; SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Pootjiespram (28. 05S 16.57E), 16.ix.1995 (F. W., S. K. and R. W. Gess), 4 ♀♀, 1 ♂ (visiting yellow flowers of *Cleome paxii* (Schinz) Gilg and Ben., Brassicaceae); Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess), 15 ♀♀, 6 ♂♂ (13 ♀♀, 3 ♂♂ visiting pale white-pink flowers of *Prenia sladeniana* (L. Bol.) L. Bol., Aizoaceae: Mesembryanthema; 2 ♀♀ visiting yellow flowers of *Gorteria* sp., Asteraceae; 1 ♂ visiting pale yellow flowers of *Cotula* sp., Asteraceae; 1♂ visiting yellow flowers of *Leysera tenella* DC., Asteraceae; 1 ♂ in deep-violet flower of *Peliostomum leucorrhizum* E. Mey. ex Benth., Scrophulariaceae); Richtersveld, 4 km N Annis River crossing by road to Sendelingsdrif (28.23S 16.55E), 21.ix.1997 (F. W. and S. K. Gess), 5 ♀♀, 6 ♂♂ (visiting dark-pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembryanthema); Namaqualand: 39 km E Springbok [29.31S 18.17E], 1.x.1997 (F.W. and S. K. Gess), 1 ♂ (visiting pink flowers of *Stoeberia* sp., Aizoaceae: Mesembryanthema)–[all AMG].



Figs 6–9. *Quartinia codoni*: 6, ♀, dorsal view (× 12); 7, ♂, dorsal view (× 12); 8, ♀, head, front view (× 26); 9, ♂, head, front view (× 26).

Geographic distribution.—Known from Namibia from the extreme south of the Desert and Succulent Steppe (Winter rainfall region) of Giess (1971) and from the adjoiniing Northern Cape of South African from the Richtersveld and Northern Bushmanland.

Floral associations.—Recorded from five plant families: Aizoaceae: Mesembryanthema (*Brownanthus*, *Drosanthemum*, *Juttadinteria*, *Prenia*, *Stoeberia*); Asteraceae (*Cotula*, *Gorteria*, *Leysera*, *Pteronia*, *Tripteris*); Brassicaceae (*Cleome*); Geraniaceae (*Sarcocaulon*); Scrophulariaceae (*Aptosimum*, *Peliostomum*).

Nesting.—Unknown.

Quartinia codoni Gess, new species
(Figs 6–9)

Quartinioides sp. 2A. Gess and Gess, 2003: 74 (flower visiting).

Diagnosis.—Medium to large (4.2–5.0 mm). Fore wing with Cu1a and *2m-cu* present but attenuate, much thinner then other veins, and with *2m-cu* interrupted before reaching M. Both sexes with oblique pale streak on each side of vertex in addition to pale streak on temple behind upper part of eye (Figs 6, 7). Male with posterior margin of sterna VII + VIII medially with a narrow, black, rectangular lamella; distal margin of lamella extending posteriorly as far as postero-lateral angles of sterna.

Description.—*Female* (Figs 6, 8): Black. Yellow are: transverse mark (in many specimens bilobed, in some specimens reduced to pair of small to minute spots) on proximal border of clypeus flanking clypeo-frontal suture; small spot (in some specimens absent) on each side of clypeal disk; pair of spots on lower half of frons, entire ocular sinus; streak on temple behind upper part of eye; oblique streak on each side of vertex (Fig. 6) (in great majority of specimens separate from streak behind eye, in small minority narrowly joined); entire hind margin of pronotum (to postero-dorsal angle) and spot on humeral angle of same (spot in some specimens narrowly joined to anterior transverse band); spot (in many specimens crescent-shaped) antero-laterally on mesonotum, narrow streak (in some specimens absent) laterally flanking tegula and pair of sub-triangular spots (in some specimens joined to form a broadly U-shaped transverse

marking; in a minority of others reduced to a scattering of minute spots or totally absent) postero-medially on same; posterior band on scutellar disk (widened and rounded laterally and anteriorly pointed medially–thus leaving a bilobed black area basally); scutellar lamella laterally; large band anteriorly on mesopleuron; propodeal angle; posterior bands reaching sides on terga I–V (those on terga II–V generally widened laterally and medially); apex of femur and base of tibia of all legs. Various shades of reddish-brown are: labrum, mandible; antenna, terga (other than for yellow bands), sterna, most of legs. Wings hyaline; veins brown.

Length 4.4–5.0 mm (average of 5: 4.7 mm); length of fore wing 2.7–3.2 mm (average of 5: 3.0 mm); hamuli 5.

Head in front view 1.33 × as wide as long (average of 3); finely microreticulate (shagreened), moderately shiny, without obvious punctures. POL: OOL = 1: 0.8. Clypeus 1.6 × as wide as long; anterior margin shallowly and widely emarginate; antero-lateral angles rounded.

Mesosoma microreticulate, moderately shiny, with small, shallow punctures variously separated by less than to twice puncture width.

Gaster microreticulate, moderately shiny, with small shallow punctures decreasing in size posteriorly.

Setae on head and mesosoma fine, short; those on gaster, particularly on tergum I, longer, posteriorly directed.

Male (Figs 7, 9): Black. Yellow are: underside of antenna; mandible except extreme base); labrum; clypeus; narrow paraocular streak (ventrally angularly widened at mandibular articulation and dorsally merging with infilling of ocular sinus); transverse band across lower half of frons, consisting of infilling of ocular sinus of each side fused with pair of large subquadrate markings (leaving black only a streak above antennal insertion and a small, sub-oval, medio-ventral spot and in some specimens a thin median line above it); in some specimens an upward extension ot the transverse band along inner upper margin of eye; streak on temple behind upper part of eye; oblique streak on each side of vertex (Fig. 7) (in great majority of specimens separate from streak behind eye, in small minority narrowly joined to it and/or to streak along inner upper margin of eye); anterior margin of pronotum fused laterally with large humeral spot; entire hind margin of pronotum (to postero-dorsal angle; crescent-shaped marking antero-laterally on mesonotum, narrow streak laterally flanking tegula and pair of subtriangular spots (in most specimens joined to form a broadly U-shaped transverse marking) postero-medially on same (these discrete markings in many specimens bilaterally uninterruptedly fused by the narrow posterior extension of the ends of each antero-lateral crescent to join respectively the narrow parategular streak and the anterior extension of each arm of the U-shaped transverse postero-medial marking); posterior band on scutellar disk (widened and rounded laterally and anteriorly pointed medially–thus leaving a bilobed black area basally); scutellar lamella laterally; large band anteriorly on mesopleuron; propodeal angle; posterior bands reaching sides on terga I–VI (that on I wider than those on II–VI; all widened laterally and medially); apex of femur and base of tibia of all legs. Various shades of reddish-brown are: upper surface of antenna, terga other than for yellow bands (I–V generally dark to very dark medially, lighter laterally; VI light, particularly around incision); sterna, most of legs.

Melanistic specimens, particularly those from the Richtersveld have the basal half of the mandible black; lack most or all of the paraocular streak; have the band across the lower half of the frons reduced to the infilling of the ocular sinus and to a pair of discrete subquadrate markings; and do not show the uninterrupted fusion of the mesonotal markings.

Length 4.2–4.3 mm (average of 5: 4.25); length of fore wing 2.8 mm; hamuli 5.

Head in front view 1.38 × as wide as long (average of 3); finely microreticulate (shagreened), moderately shiny, without obvious punctures. POL: OOL = 1: 0.9. Clypeus 1.6 × as wide as long; anterior margin shallowly and widely emarginate; antero-lateral angles rounded.

Mesosoma and gaster microreticulate and punctured as in female. Setation of head, mesosoma and gaster as in female.

Tergum VII apico-medially with a V-shaped incision; sides of incision and margin of tergal lobes flanking incision distinctly lamellate. Posterior margin of sterna VII + VIII medially with a narrow, black, rectangular lamella; distal margin of lamella extending posteriorly as far as postero-lateral angles of sterna.

Etymology.—The name *codoni*, genitive singular, is formed from the generic name of the plant *Codon royenii* L. (Boraginaceae), in the flowers of which the wasp was found in large numbers at several localities.

Material examined.—Holotype: ♂, NAMIBIA: E of Oranjemund, 37 km from checkpoint on road to Sendelingsdrif (28.23S 16.44E), 24.ix.1997 (F. W. and S. K. Gess) (visiting white flowers of *Codon royenii* L., Boraginaceae) [AMG]. Paratypes: NAMIBIA: 10 km S of Rosh Pinah (28.02S 16.50E), 15.x.2000 (F. W. and S. K. Gess), 3 ♀♀ (visiting white flowers of *Codon royenii* L., Boraginaceae); E of Oranjemund, 37 km from checkpoint on road to Sendelingsdrif (28.23S 16.44E), 24.ix.1997 (F. W. and S. K. Gess), 59 ♀♀, 83 ♂♂ (48 ♀♀ and 83 ♂♂ visiting white flowers of *Codon royenii*; 11 ♀♀ visiting white flowers of *Mesembryanthemum* sp., Aizoaceae: Mesembryanthema)–[all AMG]. SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess), 4 ♀♀, 4 ♂♂ (1 ♀, 1 ♂ [*in copula*] visiting white flowers of *Codon royenii*; 2 ♀♀, 2 ♂♂ [one pair *in copula*] visiting pale white-pink flowers of *Prenia sladeniana* (L. Bol.) L. Bol., Aizoaceae: Mesembryanthema; 1 ♀, 1 ♂ in deep violet flowers of *Peliostomum leucorrhiza* E. Mey. ex Benth., Scrophulariaceae); Richtersveld National Park, Paradise Kloof (28.19S 17.01E), 22.ix.1995 (F. W., S. K. and R. W. Gess), 1 ♀ (visiting pale white- pink flowers of *Prenia sladeniana*); Richtersveld: 24 km N of Annis River crossing by road to Sendelingsdrif (28.14S 16.55E), 21.ix.1997 (F. W. and S. K. Gess), 4 ♀♀, 2 ♂♂ (all visiting white flowers of *Codon royenii*)–[all AMG].

Geographic distribution.—Appears to be restricted to the winter rainfall area (Desert and Succulent Steppe of Giess, 1971) of south western Namibia and the adjacent Richtersveld of the Northern Cape of South Africa.

Floral associations.—Most commonly found in the flowers of *Codon royenii* L. (Boraginaceae, formerly in Hydrophyllaceae); less commonly visiting flowers of Aizoaceae: Mesembryanthema (*Mesembryanthemum, Prenia*) and Scrophulariaceae (*Peliostomum*). Within the large, cup-shaped, flowers of *Codon royenii* these small wasps were frequently present in numbers, sunning themselves, mating, drinking nectar and collecting pollen.

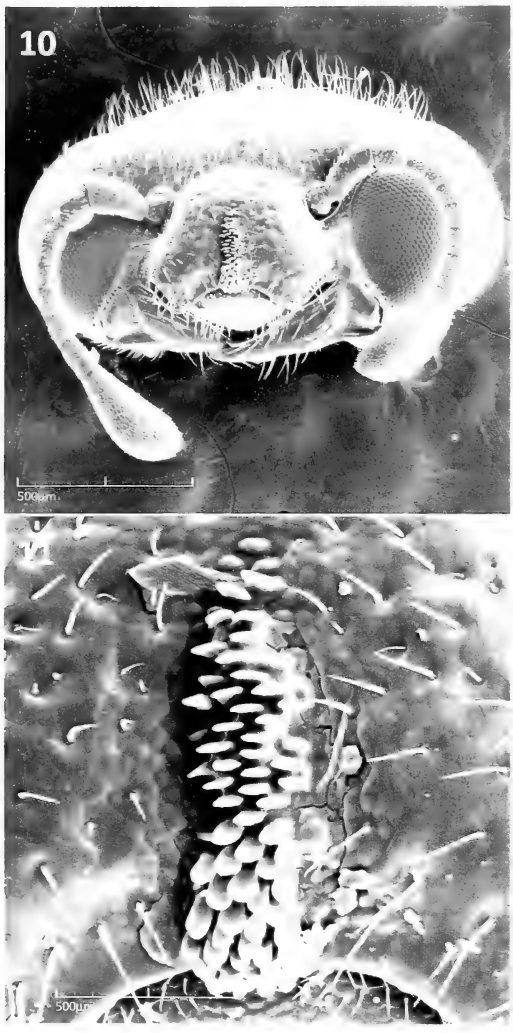
Nesting.—Unknown.

Discussion.—Reminiscent of *Q. laeta* von Schulthess but distinguishable from that species in both sexes by its larger size (4.2–5.0 mm as compared with 3.5–4.0 mm) and by the possession of an oblique pale streak on each side of vertex. In the male distinguishable also by the differently shaped posterior margin of sterna VII + VIII (medially with a narrow, black, rectangular lamella extending posteriorly as far as level of postero-lateral angles of sterna, as compared with considerably wider, black, rectangular lamella extending posteriorly short of the level of the postero-lateral angles of the sterna.

Quartinia diana (Richards)
(Figs 10, 11)

Quartinioides diana Richards, 1962: 178. Holotype: ♀, Namibia: Aus (BMNH).

Quartinia ?diana (Richards): Gess and Gess, 2003: 59 (flower visiting).



Figs 10, 11. *Quartinia diana*: 10, ♂, head, ventro-frontal view; 11, ♂, portion of clypeus showing median "brush" of modified setae.

Diagnosis.—Medium to large (4.4–4.6 mm). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula with posterior inner corner almost rounded, yellowish brown. Both sexes with head, mesosoma and gaster brightly shiny; mesoscutum and scutellum very sparsely punctured. Head, dorsal aspect of pronotum, postero-lateral aspects of propodeum, and gaster with distinct, outstanding, fine, pale setae, longest and most dense on terga. Male with a unique vertical "brush" of short, stout, black, semi-porrect to porrect setae on lower half of clypeus (see also description below) (Figs 10, 11).

Description.—Male (hitherto undescribed): Very similar in coloration and colour pattern to female, most noticeably differing in the following characters. Labrum, most of disk of clypeus pale yellow (except area below antennal insertion and along midline on lower half); the latter dark area narrowly and slightly depressed and, as seen under a binocular microscope, apparently closely set with a vertical "brush" of short, stout, black, semi-porrect to porrect setae; setae as seen with the aid of a scanning electron microscope much modified, flattened, widened and distally rounded (Figs 10, 11); "brush" at its lower end overhanging base of labrum. Terminal two flagellomeres black throughout, contrasting markedly with pale lower surface of preceding flagellomeres. Frons with a pair of brown spots above clypeofrontal suture. Mesoscutum and scutellum in most specimens with fine setae as on other parts of the body. Tergum VII posteriorly with a short median slit. Parameres unusually robust.

Material examined.—NAMIBIA: Aus (Pad C 13) [26.40S 16.15E], 8.xii.1994 (M. Kuhlmann), 6 ♀♀ [5 ♀♀ Coll. M. Kuhlmann, London, 1 ♀ AMG]; SW Klein-Aus Vista (26.44S 16.10E), 24.ix.2003 (F. W. and S. K. Gess), 1 ♀ (visiting violet flowers of *Peliostomum leucorrhizum* E. Mey. ex Benth., Scrophulariaceae) [AMG]; E of Oranjemund, 37 km from checkpoint on road to Sendelingsdrif (28.23S 16.44E), 24.ix.1997 (F. W. and S. K. Gess), 2♀♀, 2 ♂♂ (1 ♀, 2 ♂♂ visiting white flowers of *Psilocaulon* sp., Aizoaceae: Mesembryanthema; 1 ♀ visiting white flowers of *Codon royeni* L., Boraginaceae) [AMG]; SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R .W. Gess), 10 ♀♀, 11 ♂♂ (7 ♀♀ 7 ♂♂ in deep violet flowers of *Peliostomum leucorrhizum*; 1 ♀ on pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembryanthema; 1 ♀ on yellow flowers of Aizoaceae: Mesembryanthema; 1 ♂ on blue rayed *Felicia* sp., Asteraceae; 1 ♀ and 1 ♂, *in copula* on yellow flowers of *Gorteria* sp., Asteraceae; 2 ♂♂ without flower visiting data);

same locality, 6.ix.1996 (F. W., S. K. and R. W. Gess), 2 ♂♂ (on ground near flowering *Peliostomum* sp., Scrophulariaceae); Richtersveld National Park, Paradise Kloof (28.19S 17.01E), 22.ix.1995 (F. W., S. K. and R. W. Gess), 1 ♂ (on pink flowers of *Drosanthemum* sp.)–[all AMG].

Provenance of specimens examined by Richards (1962).—NAMIBIA: Aus (16 ♀♀).

Geographic distribution.—Appears to be restricted to the winter rainfall area (Desert and Succulent Steppe of Giess 1971) of south western Namibia and the adjacent Richterveld of the Northern Cape of South Africa.

Floral associations.—Most commonly found in or near the flowers of *Peliostomum* (Scrophulariaceae), less commonly visiting the flowers of Aizoaceae: Mesembryanthema (*Drosanthemum, Psilocaulon* and an unidentified species), Asteraceae (*Felicia, Gorteria*) and Boraginaceae (*Codon*).

Nesting.—Unknown.

Discussion.—Richards (1962: 179) correctly states that "in its relatively long pubescence and brightly shining integument, this species is very distinct from other species of the genus". Furthermore the male's vertical "brush" of short, stout, black, porrect setae on the lower half of clypeus is unique and therefore diagnostic. Whereas the mesoscutum of the male has setae, only vestiges, mainly around the edges, are present on that of the female. Possibly denudation of the mesoscutal setae of the female results from her nesting activity.

Quartinia maculipennis Gess, new species (Fig. 12)

Quartinia sp. nov. mac, Gess and Gess, 2003: 60 (flower visiting).

Diagnosis.—Small (2.8–3.1 mm long). Fore wing with Cu1a and 2*m-cu* thin but not appreciably more so than other veins. Tegula with posterior inner corner inwardly produced. Both sexes with anterior portion of wing tip (from distal third of marginal cell) distinctly infuscate (Fig. 12).

Fig. 12. *Quartinia maculipennis*: ♀, ventro-lateral view (× 19) showing macula on fore wing.

Male with tergum VII not terminally emarginate as is usual in the genus but triangular and somewhat hood-like, subcarinate in midline over distal half and ending apically in a pronounced, shiny, downcurved, nose-like projection.

Description.—Female (Fig. 12): Black. The following are yellowish-white: median section of mandible (to variable degree), underside of antenna (except last flagellomere); medially interrupted anterior margin of pronotum and postero-dorsal region of same; humeral marking; elongate mark anteriorly on mesopleuron; lateral spot on disk of scutellum and medially interrupted band on lamellate margin of same; tegula (with exception of median testaceous area); posterior bands (not reaching sides) on terga I–IV or V (V in some specimens testaceous); apex of femur, tibia (other than for variable amount of black at mid length), and tarsomeres I–IV of all legs.

Wings with venation brown; fore wing with 2*m-cu* not appreciably thinner than other veins; membrane almost hyaline but with anterior portion of wing tip (from distal third of marginal cell) distinctly infuscate (Fig. 12).

Length 2.8–3.0 mm (average of 5: 2.9 mm); length of fore wing 1.9–2.0 mm; hamuli 4–5.

Head in front view 1.18 × as wide as long; POL: OOL = 1: 1.1. Clypeus, frons,

thorax and gaster microreticulate; mesonotum with indistinct, small, shallow punctures. Head and thorax a little shiny, gaster more so. Tegula with posterior inner corner inwardly produced.

Male: Coloration and markings very similar to those of female, with additional yellowish-white markings as follow: labrum (if not testaceous); disk of clypeus; narrow transverse supraclypeal marking (not reaching antennal sockets) adjoining clypeo-frontal suture. Infuscation of fore wing tip as in female (Fig. 12).

Length 3.1 mm (2 specimens); length of fore wing 1.9 mm; hamuli 4–5.

Tergum VII not terminally emarginate as is usual in the genus but triangular and somewhat hood-like, subcarinate in midline over distal half and ending apically in a pronounced, shiny, downcurved, nose-like projection. Sternum II, posterior to groove, transversely swollen over almost entire width but especially so medially, anteriorly falling very steeply into groove and posteriorly somewhat less steeply to hind margin of segment.

Etymology.—The name serves to draw attention to the infuscate spot at the tip of the fore wing.

Material examined.—Holotype ♂, NAMIBIA: Gaub River bed in Gaub Pass (23.29S 15.46E), 14.iv.1988 (F. W. and S. K. Gess) (visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae) [AMG]. Paratypes: NAMIBIA: between Kuiseb and Gaub passes (23.27S 15.46E), 22.iii.1999 (F. W. and S. K. Gess), 1 ♀, 1 ♂ (visiting yellow flowers of *Zygophyllum simplex* ; Gaub River bed in Gaub Pass (23.29S 15.46E), 14.iv.1988 (F. W. and S. K. Gess), 1 ♂ (visiting yellow flowers of *Zygophyllum simplex*); Gaub Pass (23.30S 15.46E), 19.iii.1997 (F. W. and S. K. Gess), 6 ♀♀ (visiting yellow flowers of *Zygophyllum simplex*)–[all AMG]; Namib National Park, Homeb [locality not traced], 23.i.1988 (R. Miller and L. Stange), 2 ♀♀, 1 ♂ [FSCA].

Geographic distribution.—Known only from Namibia, from the Central Namib and the Semi-desert and Savanna Transition of Giess (1971).

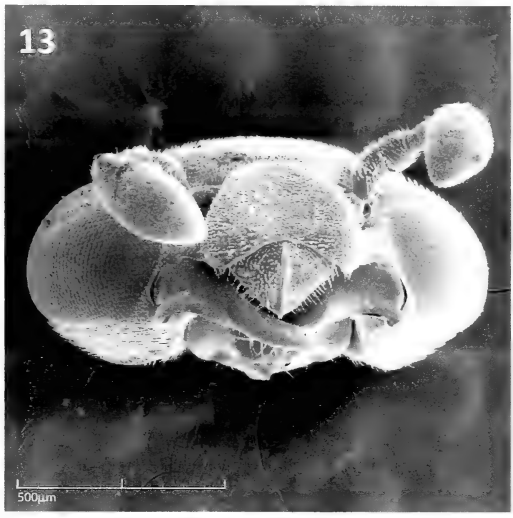


Fig. 13. *Quartinia mandibulata*: ♂, head, ventro-frontal view showing mandibles.

Floral associations.—Known only in association with *Zygophyllum simplex* L. (Zygophyllaceae).

Nesting.—Unknown.

Quartinia mandibulata Gess, new species (Fig. 13)

Quartinia sp. N3 (*partim*), Gess and Gess, 2003: 74 (flower visiting).

Diagnosis.—Small (3.2 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins, and with 2 *m-cu* interrupted before reaching M. Tegula with posterior inner corner inwardly produced. Male black with yellowish-white markings and with legs predominantly light yellow-ochre. Mandible in basal half markedly emarginate externo-laterally (Fig. 13); clypeal disk slightly depressed antero-medially; labrum carinate.

Description.—Male: Black. The following are yellowish-white: basal emargination of mandible (in all but one specimen); labrum; clypeus (other than below antennal socket); large mark (in some specimens bilobed dorsally) on frons immediately above clypeus; streak almost filling ocular sinus and extending down paraocular area

(leaving a narrow black streak above antennal socket); broad streak on temple behind upper part of eye carried down narrowingly along hind margin of eye towards or to mandibular articulation and in some specimens crossing malar space to join bottom of inner paraocular streak; underside of scape, pedicel and flagellomeres I–VII and part of VIII (most obvious on VI and VII and contrasting markedly with black distal part of club); hind margin of pronotum; humeral spot; large, irregularly-shaped mark at top of mesopleuron: tegula other than for testaceous median area; transverse postero-medial spot on disk of scutellum and lamellate margin (medially interrupted) of same; propodeal angle; posterior bands on terga I–VI (not quite reaching sides and all but I more or less expanded medially and laterally). The following are yellow-ochre: mandible (other than yellowish-white basal part and reddish-brown tip; entire legs (other than in some specimens reddish-brown tarsomere 5). In the majority of specimens the ground colour of the mesosoma (but not the mesonotum and scutellum) and the gaster is dark brown rather than black. Wings subhyaline; veins brown.

Length 3.2 mm; length of fore wing 2.1 mm; hamuli 4.

Head in front view 1.22–1.28 × as wide as long (average of three specimens: 1.26 ×); finely microreticulate (shagreened), moderately shiny. POL: OOL = 1: 0.9. Clypeus 1.55–1.60 × as wide as long (average of three specimens: 1.58 ×), steeply raised laterally above paraocular areas and with disk slightly depressed antero-medially; dorsal margin rising to slightly exceeding level of an imaginary line joining top of antennal sockets; distal margin widely and shallowly emarginate, narrowly lamellate. Labrum with a well developed median carina. Mandible in basal half markedly but smoothly emarginate externo-laterally; in front view sinuate (Fig. 13).

Mesosoma microreticulate, moderately shiny, without obvious punctures.

Gaster microreticulate with very indistinct shallow punctures, moderately shiny. Tergum VII with a deep and narrow V-shaped emargination or incision; lobes flanking incision apically pointed but narrowly rounded, slightly upturned. Sterna VII + VIII with a very small, black protruberance.

Setation of head and mesothorax and gaster inconspicuous, fine, short; that on tergum I a little more obvious.

Female.—No females could with certainty be associated with the males here described.

Etymology.—The name serves to draw attention to the unusually formed mandible of the male.

Material examined.—Holotype ♂, NAMIBIA: Gaub Pass (23.30S 15.46E), 19.iii.1997 (F. W. and S. K. Gess) (visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae) [AMG]. Paratypes: NAMIBIA: Swakopmund Dist[rict], Upper Panner Gorge (22.29S 15.01 E), 10.iv.–8.v.1984 (J. Irish and H. Liessner), 3 ♂♂ [NNIC]; Swakopmund Dist[rict], Lower Ostrich Gorge (22.30S 14.58E), 11.iii.–9.iv.1985 (J.Irish and H. Rust), 1 ♂ [NNIC]; between Kuiseb and Gaub passes (23.27S 15.46E), 22.iii.1999 (F. W. and S. K. Gess), 1 ♂ (visiting yellow flowers of *Zygophyllum simplex)* [AMG].

Geographic distribution.—Known from Namibia from localities in the Central Namib of Giess (1971).

Floral associations.—Zygophyllum simplex L. (Zygophyllaceae).

Nesting.—Unknown.

Quartinia minima von Schulthess

Quartinia minima von Schulthess, 1932:528, ♀. Holotype: ♀, Namibia: Aus (BMNH); Gess and Gess, 2003: 60 (flower visiting).

Quartinioides minima (von Schulthess) Richards, 1962: 179.

Diagnosis.—Minute to small (2.3–3.0 mm long). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula with posterior inner corner inwardly produced,

yellow (except for pale testaceous discal spot. Clypeus produced circa 0.5–1 × antennal socket diameter above level of an imaginary line joining upper margins of sockets. Both sexes with head and thorax black with moderate yellow markings; gaster predominantly yellow.

Male "face" with following pale: mandibles (other than base), labrum, clypeus to varying extent, streak in ocular sinuses (in some specimens extended ventrally onto paraocular area), pair of supraclypeal spots (in some specimens fused). Mandible not swollen at base. Labrum without any indication of a median carina, its distal margin evenly rounded. Antennal club elongate, length > 2 × width, end rounded.

Discussion and additional descriptions.— Described rather briefly by von Schulthess from a single female and redescribed in greater detail by Richards from the same specimen, this species is difficult to recognise from the literature due to several incorrect statements. Thus in Richards' key (p.171) and in his description (p.180) it is stated that the hind tibia has only one spur whereas the type actually has two: the long spur mentioned by Richards and in addition a very much shorter and thinner one. Richards (p.179) states that the head in front view is "about one quarter times longer than broad" whereas it is actually 1.21 × as wide as long. Further, he states (p.172) that the clypeus at midline is "not much shorter than maximum breadth" and (p.179) "clypeus just transverse, extreme width one-quarter longer than central length" whereas it is actually 1.5 × as wide as long.

Richards' statement that the dorsal margin of the clypeus in the centre is "well above level of antennal socket" is correct. Actually it is about one socket diameter above a line joining the dorsal margins of the antennal sockets, the head being positioned such that the vertex between the ocelli and the ventral margin of the clypeus are concurrently in focus.

A series of 77 ♀♀ and 19 ♂♂ from three localities along the seaboard of the Namib Desert are assignable to the species, the true proportions of the head and clypeus given above for the type of *minima* falling within the range established for the new material.

In order adequately to characterize the species, the following description, based on a sample of 65 ♀♀ and 19 ♂♂ from 110 km north of Swakopmund, deals in considerable detail with the colour pattern, the extent of the pale markings being variable within a population and, with regard to any individual specimen, marked development of pale markings on one body part not necessarily being accompanied by concomitant development of such on another. The recently collected specimens from the other listed localities fall within the same range of variation. All the specimens differ from the type from Aus in that the wide sinuate frontal band from one ocular sinus to the other is not developed.

Female.—Black. The following are yellowish-white: occasionally a small subbasal spot on mandible; markings on clypeus [rarely totally absent] consisting of antero-lateral spots, small antero-medial spot and occasionally a minute baso-medial spot, or of anterior margin and minute baso-medial spot, or of anterior margin and median streak connecting with baso-medial spot (to form a narrow anchor-like marking), or of wide anterior margin and upwardly widening median streak (to form a wide anchor-like marking and leaving only a pair of variably sized oblique black subantennal streaks on the otherwise pale clypeus); supraclypeal marking on frons [rarely totally absent] consisting of a pair of minute to small spots (if minute sometimes present on only one side), or of a pair of large well separated or closely approximated spots, or of a large trapezoidal patch (formed by the fusion of spots) incorporating a small black central spot; entire ocular sinus; occasionally an isolated spot or a

narrow streak (connecting with white of ocular sinus) in paraocular area flanking clypeus; post-ocular streak extending from behind top of eye or sometimes from near posterior ocellus to half way down gena; rarely a small spot at bottom of gena at mandibular insertion; rarely a small spot flanking inner margin of upper part of eye, or a band descending from postocular streak and approaching or connecting with white of ocular sinus; rarely two or more minute to small spots between and slightly posterior to hind ocelli; in one specimen a longitudinal streak on each side of anterior ocellus and extending dorsally between and slightly posterior to posterior ocelli; hind margin and humeral angle (to variable degree) or entire dorsal part of pronotum; markings on mesonotum consisting bi-laterally of postero-lateral streak adjoining tegula and often of small antero-lateral spot/spots/crescent and postero-medially of an anteriorly bipronged subrectanglar patch, or of postero-lateral streak produced to incorporate antero-lateral spots and thence recurved and directed posteriorly towards but not meeting anteriorly bipronged subrectangular patch, or of broad lateral streak anteriorly produced, recurved and broadly and smoothly connecting with postero-medial patch; tegula (other than for small clear central area); scutellar disk (other than for antero-medial posteriorly bilobed black mark or occasionally only mesoscutal/scutellar suture); scutellar lamella; central part of metanotum; large mark on upper part of pleuron; dorsal area and lateral angles of propodeum (declivity more or less bracketed with white and with small white median spot) or almost entire propodeum; all terga; terminal sterna (basal sterna variably suffused with black); coxae occasionally in part; apices or occasionally most of femora; entire tibiae; tarsomeres 1–4 (tarsomeres 5 contrastingly dark).

Length 3 mm; length of fore wing 2 mm; hamuli 4. Tongue length circa 3 mm.

Head 1.18 × as wide as long (average of 5; range 1.17–1.20). Clypeus 1.51 × as wide as long (average of 5; range 1.48–1.53); clypeal dorsal margin variably produced, attaining a level ranging from just above a line joining the dorsal margins of the antennal sockets to about one socket diameter above such a line.

Male (hitherto undescribed).–Similarly coloured to the female but with the following differences: mandible (other than black base), labrum, and occasionally entire disk of clypeus yellowish-white; frons in one specimen with white of ocular sinus and of supraclypeal spot narrowly joined (unilaterally only); mesonotum with bilateral postero- lateral streak adjoining tegula and anteriorly bipronged subrectangular postero-medial marking only; declivity of tergum 1 always black; terga II-IV usually with black anterior transverse bands (best visible in a downwardly flexed gaster); terga I-VI often with a pair of widely separated, narrow, blackish, transverse markings in posterior half.

Length 2.3–2.7 mm (average of 7: 2.4 mm); length of fore wing 1.6–1.8 mm (average of 4: 1.7 mm); hamuli 4.

Head 1.26 × as wide as long (average of 3; range 1.25–1.29).

Clypeus 1.54 × as wide as long (average of 3; range 1.46–1.62); clypeal dorsal margin attaining a level slightly above a line joining the dorsal margins of the antennal sockets; distal margin moderately emarginate and moderately lamellate; disk distolaterally with short inconspicuous setae. Labrum without any indication of a median carina, inconspicuously and sparsely setose; distal margin evenly rounded.

Tergum VII with a shallow V-shaped apical incision, the lobes defining it rounded; apical margin of sterna VII + VIII with a wide black median projection; parameres flattened, wide, distally with outer margin smoothly rounded to apex and inner margin with an emargination producing a proximal tooth and an apical hook.

Material examined.—NAMIBIA: Aus, xii.1929 (R. E. Turner), Holotype ♀ (B.M.TYPE HYM. 18.49) [BMNH]; Ugab River, coastal road (21.06S 13.34E), 17.iii.1999, 1 ♀ (visiting yellow flowers of *Galenia papulosa* (Eckl. and Zeyh.) Sond., Aizoaceae: non-Mesembryanthema); 110 km NW of Swakopmund (21.50S 14.05E), 15.iii.1999, 65 ♀♀, 19 ♂♂ (61 ♀♀, 18 ♂♂ visiting yellow flowers of *Galenia papulosa*; 3 ♀♀, 1 ♂ visiting white flowers of *Brownanthus kuntzei* (Schinz) Ihlenf. and Bittrich, Aizoaceae: Mesembryanthema; 1 ♀ visiting yellow flowers of *Tripteris microcarpa* Harv., Asteraceae); 10 km N of Swakopmund at wireless mast (22.35S 14.32E), 21.iii.1997, 11 ♀♀(visiting yellow flowers of *Galenia papulosa*); 97 km by road from Swakopmund to Usakos (22.10S 15.10E), 16.iii.2000, 2 ♀♀ (visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae)–all F. W. and S. K. Gess [AMG] (unless otherwise indicated).

Geographic distribution.—Known only from Namibia, from Aus in the Desert and Succulent Steppe of Giess (1971) and from the seaboard and interior of the Central Namib.

Floral associations.—Along the seaboard of the Central Namib very markedly associated with Aizoaceae: non-Mesembryanthema (*Galenia papulosa*); in a drainage line within the Central Namib found on Zygophyllaceae (*Zygophyllum simplex*).

Nesting.—Unknown.

Quartinia parva Gess, new species

Quartinia sp. N4, Gess and Gess, 2003: 74.

Diagnosis.—Minute to small (2.4–2.8 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins, and with 2*m-cu* interrupted before reaching M. Tegula with posterior inner corner rounded and inwardly produced. Distinguished from other species by a combination of characters: its small size, tegular shape, and colour pattern.

Description.—Female: Black. The following are yellowish-white: most of under side of antenna; minute dot or very narrow streak (in small minority of specimens only) at bottom of ocular sinus; small streak (effaced in some specimens) on temple behind upper part of eye; hind margin of pronotum (continuous to postero-dorsal angle or interrupted before reaching latter) and humeral angle of same; small streak at top of mesopleuron; anterior and posterior parts of tegula (median part testacious); three spots on scutellar disk–a baso-lateral pair and a larger postero-medial one (in some specimens with baso-lateral pair effaced, in others with three spots narrowly fused); scutellar lamella laterally; propodeal angle; posterior bands (expanded medially and laterally and reaching sides) on terga I–V; apex of femur and base of tibia of all legs. Various shades of reddish-brown are: mandible; most of upper side of antenna; legs (other than for pale parts indicated above and darker tarsomere V) Wings subhyaline; veins brown.

Length 2.8 mm (average of 3); length of fore wing 1.9 mm (average of 3); hamuli 4.

Head in front view 1.38 × as wide as long (average of 3), finely microreticulate (shadreened), moderately shiny; frons and vertex with very indistinct, shallow punctures; POL: OOL = 1: 0.9. Clypeus 1.7 × as wide as long; anterior margin widely and shallowly emarginate.

Mesosoma microreticulate, moderately shiny, with scattered small punctures (more obvious than on head). Gaster moderately shiny.

Male: Black. The following are yellowish-white: labrum; clypeus; large sub-oval mark, encompassing a small black median spot, on lower part of frons contiguous with yellowish-white clypeus (in a few specimens mark is narrowly divided into two by a thin vertical black line passing through the median black spot); streak of variable shape and size in lower half of ocular sinus; small streak (effaced in some specimens) on temple behind upper part of eye; hind margin of pronotum (continuous to postero-dorsal angle or interrupted before reaching latter) and humeral angle of same; small streak at top of meso-

pleuron; anterior and posterior parts of tegula (median part testacious); three spots on scutellar disk–a baso-lateral pair and a larger postero-medial one (in some specimens with baso-lateral pair effaced, in others with three spots narrowly fused); scutellar lamella laterally; propodeal angle; posterior bands (expanded medially and laterally and reaching sides) on terga I–VI; in some specimens a small median mark on tergum VII; apex of femur and base of tibia of all legs. Various shades of reddish-brown are: mandible; most of antenna (except most of club); leg (other than for pale parts indicated above and darker tarsomere V) Wings subhyaline; veins brown.

Length 2.4 mm (average of 3); length of fore wing 1.7 mm (average of 3).

Head in front view 1.34 × as wide as long (average 3 specimens). POL: OOL = 1: 0.8. Clypeus 1.7 × as wide as long (average of 3); dorsal margin attaining a level only slightly exceeding an imaginary line joining dorsal margins of antennal sockets.

Tergum VII with a shallow V-shaped emargination and with lobes flanking it widely rounded. Sterna atuberculate.

The above descriptions are based on the large sample taken of the population at the Swakop River and take cogniscence of variations within that population. The specimens from further inland (34 km SW of Usakos and between Kuiseb and Gaub passes) are generally more melanistic and exhibit, for example, a reduction or total absence of the pale spot on the humeral angle.

Etymology.—The name *parva*, a Latin female adjective meaning small, refers to the size of the species.

Material examined.—Holotype: ♂, NAMIBIA: Swakop River at bridge near mouth (22.42S 14.32E), 12.iv.1998 (F. W. and S. K. Gess) (visiting deep pink flowers of *Galenia papulosa* (Eckl. and Zeyh.) Sond., Aizoaceae: non-Mesembryanthema and yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae) [AMG]. Paratypes: NAMIBIA: 34 km SW of Usakos (22.02S 15.17E), 22.iii.1997 (F. W. and S. K. Gess), 3 ♀♀, 1 ♂ (1 ♀ visiting yellow flowers of *Zygophyllum simplex*; 2 ♀♀, 1 ♂ visiting purplish pink flowers of *Sesuvium sesuvioides* (Fenzl) Verdc., Aizoaceae: non- Mesembryanthema); between Kuiseb and Gaub passes (23.24S 15.50E), 22.iii.1999 (F. W. and S. K. Gess), 3 ♀♀ (visiting white flowers of *Zygophyllum cylindrifolium* Schinz); between Kuiseb and Gaub passes (23.27S 15.46E), 22.iii.1999 (F.W. and S. K. Gess), 1 ♂ (visiting yellow flowers of *Zygophyllum simplex*); Swakop River at bridge near mouth (22.42S 14.32E), 12.iv.1998 (F. W. and S. K. Gess), 62 ♀♀, 11 ♂♂ (visiting deep pink flowers of *Galenia papulosa* and yellow flowers of *Zygophyllum simplex*)–[all AMG].

Geographic distribution.—Known from Namibia from localities in the Semi-desert and Savanna Transition (Escarpment Zone) and the Central Namib of Giess (1971).

Floral associations.—Aizoaceae: non-Mesembryanthema (*Galenia papulosa* and *Sesuvium sesuvioides*) and Zygophyllaceae (*Zygophyllum cylindrifolium* and *Z. simplex*).

Nesting.—Unknown.

Quartinia poecila von Schulthess

Quartinia poecila von Schulthess, 1930: 327, fig. 2, ♀, ♂. Lectotype: ♂ [B.M.TYPE HYM. 18.45b], Namibia: Swakopmund (BMNH); Gess and Gess, 2003: 61 (flower visiting).

Quartinioides poecila (von Schulthess): Richards, 1962: 180; Gess and Gess, 1989: 128; Gess, S. K., 1996: Appendices 1 and 2 (flower visiting).

Quartinioides sp. H: Gess and Gess, 1989: 130; Gess, S. K., 1996: Appendices 1 and 2 (flower visiting).

Diagnosis.—Small to medium sized (2.7–4.0 mm long). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula with posterior inner corner markedly angular and somewhat inwardly produced, white (except for pale testaceous discal spot). Clypeus produced circa 0.5–>1 × antennal socket diameter above level of an imaginary line joining upper margins of sockets. Head, thorax and gaster black with white or yellow markings; pale markings

often separated from black by pale reddish. Male with pale "face" comprising mandibles, labrum, clypeus, paraocular areas and frons (upper margin of pale area varying from level of top of ocular sinuses to less than an ocellar width below median ocellus). Mandible somewhat swollen at base. Labrum moderately to markedly carinate, pyriform, its distal margin pointed. Antennal club short, length 2 × width, end rounded.

Discussion and additional descriptions.— The redescription by Richards of Schulthess's type material collected by Turner at Swakopmund adequately characterizes material from that locality, specimens of both sexes recently collected there closely matching the types and the description. However, in dealing with the female, Richards fails to mention the lateral streak (flanking the tegula) on the mesonotum, a marking listed by Schulthess and characteristic of the material (of both sexes) from Swakopmund, Lüderitz and the Sperrgebiet.

Material from localities other than the type locality shows that the species is subject to considerable variation in appearance, expressed principally in an increase in the extent of the pale markings in specimens from Lüderitz and particularly from inland in the Sperrgebiet and a reduction of the pale markings in specimens from the southern part of the distributional range.

Thus in females from Lüderitz the basal third of the clypeus is white as is a pair of antero-lateral spots; on the frons there is an upward extension along the inner orbits of the pale markings in the ocular sinuses. Females from inland in the Sperrgebiet in addition have the black areas on the dorsal aspect of the pronotum (as seen in the Swakopmund specimens) reduced to light reddish. Males from inland in the Sperrgebiet show more striking differences: the clypeus and the pale area on the frons are yellow rather than white as in males from the coast, both north and south, and the streak on the gena consistently extends down to the mandibular articulation rather than being limited to behind the eye dorsally. As in the females, the dorsal aspect of the pronotum is yellow and light reddish and there is a tendency for the better development of light markings on the mesopleuron and mesoscutum.

In females from the coast south of the mouth of the Orange River the clypeus is usually unmarked but some specimens from between Alexander Bay and Port Nolloth have a reduced transverse basal marking and two specimens from Hondeklip Bay have a median subbasal white spot and a pair of small antero-lateral white spots respectively. The white area in the ocular sinus is somewhat smaller; the two spots on the frons though usually present may be reduced or rarely even absent; the streak behind the eye is shorter and narrower; the humeral spot is smaller and the white posterior margin of the pronotum is medially and mid-laterally interrupted; the mesoscutal markings are totally effaced; the white of the scutellar disk is progressively reduced, being represented by fused postero-median and antero-lateral spots, by separate subtriangular or rounded postero-medial and antero-lateral spots, or by a single postero-median spot; the white of the central area of the metanotum is effaced; the spot on the dorsal half of the prepectus and the streaks dorsally on the propodeum are moderately to greatly reduced; the preapical bands on the terga are narrower (though widened medially and laterally on II–IV or II–III) and interrupted on V or IV; the white of VI is reduced to a pair of spots, or the white of V and VI is totally effaced. The reddish suffusion margining most of the white marks as in specimens from Swakopmund and Lüderitz is very much reduced or totally absent in specimens from further south.

Males show a similar progressive north to south reduction in the pale markings, some specimens from Hondeklip Bay

having not only the mesoscutum but also the scutellum and propodeum entirely black and the transverse posterior bands other than on tergum I barely represented. In all specimens, however, the white mandibles and the characteristic "face" comprising the white labrum, clypeus, paraocular areas and frons is preserved though in southern specimens the upper margin of the "face" does not extend above the level of the top of the ocular sinus.

Morphologically both sexes, but particularly the males, show some variation in the ratio of head width: length, the ratio of clypeus width: length, and the distance that the base of the clypeus rises upwards above the level of the antennal sockets. In comparison with males from the coast (Swakopmund and north of Port Nolloth), males from inland in the Sperrgebiet generally have a relatively wider head and clypeus, a clypeus that rises a shorter distance above the antennal sockets, and a less pronounced carina on the labrum. However, in view of the absence of corroborative characters in the females, and the variation of the relative proportions of head and clypeus (cutting across those mention above) present in the males of the Hondeklip Bay population, the possibility that the Sperrgebiet population might be specifically distinct cannot be upheld.

A small series of females from south east of Keetmanshoop in Namibia, determined by J. M. Carpenter as *Q. poecila* and examined by myself, appears to be yet another manifestation of this protean species. Like those from the coast south of the mouth of the Orange River the specimens are melanistic when compared with those from the type locality, but within the sample show some variation. All the specimens have the head and mososoma black with yellowish-white markings and lack any reddish replacement of the black. The frons (except in one specimen in which immaculate), ocular sinus, gena, pronotum, tegula, mesopleuron, scutellar lamella, and propodeal angle are similarly marked to the type, however, the clypeus may or may not have a large dorso-medial spot. Mesoscutal markings are absent except, in most specimens, for a posteromedial spot of varying size. The scutellum may have the typical marking reduced to three separate spots.

Material examined.—NAMIBIA: Swakopmund, 2–4.iv.1928 (R. E. Turner), Lectotype ♂ (B.M.TYPE HYM. 18.45b), Paratype ♀ (B.M.TYPE HYM. 18.45a) [BMNH]; Swakop R(iver), S side of mouth (22.42S 14.32E), 20.iii.1997, 1 ♀, 1 ♂ (both visiting white flowers of *Zygophyllum stapffii* Schinz, Zygophyllaceae); same locality, 12.iv.1998, 2 ♀♀ (both visiting deep pink flowers of *Galenia papulosa* (Eckl. and Zeyh.) Sond., Aizoaceae: non-Mesembryanthema and yellow flowers of *Zygophyllum simplex* L.); Lüderitzbucht, near Agate Beach (26.37S 15.11E), 29.ii.2000, 2 ♀♀ (visiting white flowers of *Zygophyllum clavatum* Schltr. and Diels,); Lüderitzbucht, near Diaz Point (26.39S 15.05E), 1.iii.2000, 3 ♀♀ (visiting pink flowers of *Brownanthus* sp., Aizoaceae: Mesembryanthema); Lüderitz Küste [circa 26.40S, 15.19E], 7.xii.1994 (M. Kuhlmann), 1 ♀ [Coll. M. Kuhlmann, London]; 30 mi[les] S. E. Keetmanshoop [circa 26.51S 18.34E], 23.x.1968 (J. G. Rozen and E. Martinez), 10 ♀♀ [AMNH]; Sperrgebiet, Tsabiams (27.10S 15.39E), 12.ix.2005 (F. W. and S. K. Gess), 26 ♀♀, 2 ♂♂ (1 ♀ visiting pink flowers of *Sarcocaulon patersonii* (DC.) G. Don., Geraniaceae); 25 ♀♀, 2♂♂ attracted to white insect net); Sperrgebiet, Klinghardtberge, Tsabiams Camp (27.10S 15.42E), 4.ix.2002, 5 ♀♀, 2 ♂♂ (5 ♀♀, 1 ♂ visiting yellow flowers of *Dimorphotheca polyptera* DC., Asteraceae; 1 ♂ visiting yellow flowers of *Grielum sinuatum* Licht. ex Burch., Neuradaceae); Sperrgebiet, Klinghardtberge, SE of Tsabiams (27.10S 15.42E), 20.ix.2003, 16♀♀, 27 ♂♂ (visiting yellow flowers of *Grielum sinuatum*); Sperrgebiet, Klinghardtberge, SE of Tsabiams (27.11S 15.42E) 20.ix.2003, 1 ♂ (visiting yellow flowers of *Grielum sinuatum*); Sperrgebiet, Klinghardtberge (27.14S 15.43E), 1.ix.2002, 3 ♀♀ (visiting yellow flowers of *Pteronia pomonae* Merxm., Asteraceae); Sperrgebiet, Klinghardtberge (27.14S 15.44E), 2.ix.2002, 4 ♀♀, 1 ♂ (3 ♀♀, 1 ♂ visiting apricot coloured flowers of *Phyllobolus oculatus* (N. E. Br.) Gerbaulet, Aizoaceae: Mesembyanthema; 1 ♀ visiting yellow flowers of

Pteronia pomonae); Sperrgebiet, Klinghardtberge (27.16S 15.45E), 3.ix.2002, 1 ♀ (visiting yellow flowers of *Tripteris crassifolia* O. Hoffm., Asteraceae); Sperrgebiet, Klinghardtberge (27.16S 15.46E), 1.ix.2002, 1 ♀ (visiting yellow flowers of *Phyllobolus oculatus*); Sperrgebiet, Klinghardtberge (27.19S 15.46E), 11.ix.2005 (F. W. and S. K. Gess). 35 ♀♀, (14 ♀♀ visiting pink flowers of *Hermannia gariepina* Eckl. and Zeyh., Malvaceae (Sterculioideae); 2 ♀♀ visiting yellow flowers of *Hermannia macra* Schltr.; 19 ♀♀ attracted to Man); Sperrgebiet, NW of Heioab (27.23S 15.56E), 19.ix.2003, 1♀, 5 ♂♂ (visiting yellow flowers of *Grielum sinuatum*); Sperrgebiet, Klinghardtberge, Nomitsas (27.27S 15.52E), 31.viii.2002, 23 ♀♀, 28 ♂♂ (20 ♀♀, 28 ♂♂ visiting yellow flowers of *Grielum sinuatum*; 3 ♀♀ visiting yellow flowers of *Oncosiphon grandiflorum* (Thunb.) Källersjö., Asteraceae); Sperrgebiet, Uguchab River, NW of Aurus Mountains (27.31S 16.12E), 17.ix.2003, 8 ♂♂ (visiting yellow flowers of *Grielum sinuatum*); Aus to Rosh Pinah (27.44S 16.43E), 25.ix.2003, 1 ♂ (visiting yellow flowers of *Grielum sinuatum*); Sperrgebiet, Chamnaub (27.45S 16.05E), 28.viii.2002, 2 ♂♂ (visiting yellow flowers of *Oncosiphon grandiflorum*). SOUTH AFRICA: NORTHERN CAPE: 60 km N of Port Nolloth (28.47S 16.38E), 27.ix.1997, 7 ♀♀, 1 ♂ (4 ♀♀ visiting pale pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembryanthema; 3 ♀♀, ♂ on ground); 24 km S of Alexander Bay (28.47S 16.38E), 11.x.2000, 2 ♀♀ (visiting pink flowers of *Drosanthemum* sp.); 28 km S of Alexander Bay (28.49S 16.39E), 11.x.2000, 2 ♀♀, 2 ♂♂ (visiting yellow flowers of Asteraceae); Port Nolloth (29.12S 16 55E), 27.ix.1997, 6 ♀♀ (visiting cream/yellow flowers of *Carpobrotus edulis* (L.) Bol., Aizoaceae: Mesembryanthema); Port Nolloth, McDougall's Bay (29.17S 16.53E), 2.x.1985, 15 ♀♀ (visiting flowers of *Drosanthemum* sp.); same locality, 11.x.1988, 2 ♀♀ (visiting flowers of *Drosanthemum* sp.); Hondeklip Bay (30.19S 17.17E), 12.x.1994, 65 ♀♀, 16 ♂♂ (visiting yellow flowers of *Herrea* sp., Aizoaceae: Mesembryanthema); 7 km WNW of Wallekraal on road to Hondeklip Bay [30.21S 17.26E], 14–16.ix.1992, 1 ♀ (visiting white flowers of *Polycarena* cf. *collina* Hiern, Scrophulariaceae)–(all F. W. and S. K. Gess) [all AMG unless otherwise indicated]; Koingnaas Mines (30. 10S 17.14E), 12–17.ix.2007, 8 ♀♀, 12–17.xi.2007, 26 ♀♀, 2 ♂♂; ditto (30.10S 17.15E), 8–14.vii.2007, 2 ♀♀, 12–17.ix.2007, 39 ♀♀, 17 ♂♂; ditto (30.12S 17.15E), 12–17.ix.2007, 3 ♀♀; ditto (30.14S 17.15E), 12–17.xi.2007, 1 ♀; ditto (30.16S 17.17E), 12–17.xi.2007, 2 ♀♀; ditto (30.18S 17.18E), 8–14.vii.2007, 2 ♀♀, 12–17.ix.2007, 16 ♀♀, 12–17.xi.2007, 2 ♀♀; ditto (30.21S 17.18E), 8–14.vii.2007, 1 ♀, 12–17.xi.2007, 3♀♀, 1 ♂; ditto (30.21S 17.20E), 8–14.vii.2007, 1 ♀, ix.2007, 13 ♀♀, 1 ♂, 12–17.xi.2007, 11 ♀♀, 1 ♂; ditto (30.22S 17.19E), 12–17.ix.2007, 14 ♀♀, 1 ♂, 12–17.xi.2007, 4♀♀; ditto (30.22S 17.20E), 8–14.vii.2007, 15 ♀♀, 1 ♂, 12–17.ix.2008, 7 ♀♀, 12–17.xi.2007, 11 ♀, 1 ♂; ditto (30.26S 17.21E), 12–16.ix.2007, 34 ♀♀, 5 ♂♂.–(all from pan traps.) (all C. Lyons *et al.*) [all AMG].

WESTERN CAPE: near Brand-se-Baai (31.22S 17.55E), 21–25.ix.2007, 2 ♀♀, 18–22.xi.2007, 4 ♀♀; ditto (31.23S 17.56E), 14–18.vii.2007, 2 ♀♀, 21–25.ix.2007, 14 ♀♀, 2 ♂♂, 17–22.xi.2007, 398 ♀♀, 48 ♂♂; ditto (31.25S 17.58E), 21–25.ix.2007, 10 ♀♀, 1 ♂, 17–22.xi.2007, 2 ♀♀; ditto (31.27S 18.00E), 21–25.ix.2007, 3 ♀♀, 17–22 .xi.2007, 16 ♀♀; ditto (31.29S 18.01E), 21–25.ix.2007, 4♀♀, 17–22.xi.2007, 11 ♀♀.–(all from pan traps.) (all C. Lyons *et al.*) [all AMG].

Geographic distribution.—Known in Namibia from the immediate vicinity of Swakopmund at the interface of the Central Namib and Southern Namib of Giess (1971), and from Lüderitzbucht, numerous localities inland in the Sperrgebiet (Diamond Area No 1) and from between Aus and Rosh Pinah, all in the Desert and Succulent Steppe. Undoubtedly occurs also in the under collected coastal areas of the Namib Naukluft Park (mostly Southern Namib) between Swakopmund and Lüderitz. Further inland (east) has also been collected south east of Keetmanshoop in the Dwarf Shrub Savanna. Known in South Africa from the Richtersveld coast between Alexander Bay and Port Nolloth, from Port Nolloth itself, and from the Namaqualand sandveld at Hondeklip Bay and at various sites north, south and east of that locality in what may be considered a southward extension of the Namib.

Floral associations.—Associated with Aizoaceae: both non-Mesembryanthema (*Galenia*) and Mesembryanthema (*Brownanthus*, *Carpobrotus*, *Drosanthemum*, *Herrea* and *Phyllobolus*), with Asteraceae (*Dimor-*

photheca, *Oncosiphon*, *Pteronia* and *Tripteris*), with Geraniaceae (*Sarcocaulon*), with Malvaceae (*Hermannia*); with Neuradaceae (*Grielum*), and with Zygophyllaceae (*Zygophyllum*), the few records of visits to the flowers of other plant families probably being incidental and of no account.

Nesting.—*Q. poecila* was observed at McDougall's Bay to nest in friable coastal dune sand.

Quartinia propinqua von Schulthess

Quartinia propinqua von Schulthess, 1932: 526, figs 2, 3, 4, female, male. Lectotype: female, Namibia: Aus (BMNH); Gess and Gess, 2003: 62 (flower visiting).

Quartinioides propinqua (von Schulthess): Richards, 1962: 199; Gess and Gess, 1989: 1; Gess, S. K., 1996: Appendices 1 and 2 (flower visiting).

Quartinioides sp. G: Gess and Gess, 1989: 128; Gess, S. K., 1996: Appendices 1 and 2 (flower visiting).

Diagnosis.—Small to medium sized (present material 2.9–4.0 mm long; 3.8–4.5 mm long according to Richards). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula with posterior inner corner absolutely rounded, white (except for pale testaceous discal spot). Head, thorax and gaster black with white markings. Female usually with mark proximally on clypeus and marking on frons limited to spot in ocular sinus; male with medially carinate labrum and most of clypeus white and marking on frons in addition to spot in ocular sinus consisting of a ventro-medial quadrate area bearing a brown spot. Scutellum always with posterior one-third to two-thirds of disk and lamellate margin white. Last tarsomere brown. Mesoscutum a little shiny, finely reticulate with small shallow punctures. Antenna of male with club very slightly hooked.

The species has been adequately described by Richards (1962).

Material examined.—NAMIBIA: W of Kamanjab, on track from Erweë to Palmfontein (19.40S 14.17E), 18.iii.2004, 4 ♀♀, 2 ♂♂ (on white flowers of *Emilia marlothiana* (O. Hoffm.) C. Jeffrey, Asteraceae); W of Kamanjab, approaching foot of Grootberg Pass (19.47S 14.17E), 18.iii.2004, 7 ♀♀, 3 ♂♂ (7 ♀♀, 1 ♂ (on white flowers of *Emilia marlothiana*; 2 ♂♂ on flowers of *Felicia anthemidodes* (Hiern) Mendonca, Asteraceae); 110 km N[N]W of Swakopmund (21.50S 14.05E), 15.iii.1999, 1 ♀ (visiting yellow flowers of *Tripteris microcarpa* Harv., Asteraceae); 10 km west of Usakos (21.59S 15.29E), 24.iv.2002, 2♀♀ (visiting yellow flowers of small daisy, Asteraceae); 117 km by road from Swakopmund to Usakos (22.02S 15.17E), 16.iii.2000, 1 ♀ (visiting pink flowers of *Sesuvium sesuvioides* (Fenzl) Verdc., Aizoaceae: non-Mesembryanthema); 74 km by road from Swakopmund to Usakos (22.19S 15.06E), 15.iii.2000, 26 ♀♀, 9 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*); 33 km by road from Swakopmund to Usakos, near Rössing Mountain (22.34S 14.49E), 15.iii.2000, 28 ♀♀ (visiting yellow flowers of *Tripteris microcarpa*), 1 ♂ (visiting white flowers of *Galenia africana* L., Aizoaceae: non-Mesembryanthema); same locality, 15.iv.2002, 2 ♀♀, 2 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*); same locality, 28.iv.2002, 11 ♀♀, 6 ♂♂(visiting yellow flowers of *Tripteris microcarpa*); same locality, 31.iii.2004, 51 ♀♀, 6 ♂♂(visiting yellow flowers of *Tripteris microcarpa*); 22 km east of Swakopmund on road to Usakos (22.36S 14,42E), 15.iv.2002, 8 ♀♀, 1♂ (visiting yellow flowers of *Tripteris microcarpa*); 16.5 km by road from Swakopmund to Usakos (22.37S 14.40E), 14.iii.2000, 13 ♀♀, 2 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*); plains south of Goanikontes (22.42S 14.47E), 16.iv.2002, 1♀, 2 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*); Solitaire (23.52S 16.00E), 30.iv.2002, 3 ♀♀, 1♂ (visiting yellow flowers of *Hirpicium* sp., Asteraceae); NW of Aus, drainage channel (26.37S 16.12E), 17.ix.2005, 1 ♀ (visiting yellow flowers of *Leysera*, Asteraceae); NW of Aus (26.37S 16.15E), 17.ix.2005, 1 ♂ (visiting yellow flowers of small daisy heads, Asteraceae); Tirasberg Road, 7.5 km N of turnoff from road to Aus (26.37S 16.21E), 20.ix.2005, 18 ♀♀, 2 ♂♂ (visiting yellow flowers of *Berkheya schinzii* O. Hoffm., Asteraceae); Plateau 38, Lüderitz (SE 2616 Cb), 4–5.iii.1972 (H7179) (no collector), 2 ♀♀ [NNIC]; 9 km west of Aus (26.39S 16.10E), 7.ix.2002, 19 ♀♀, 20 ♂♂ (visiting yellow flowers of *Berkheya schinzii*); Klein-Aus Vista (26.39S 16.15E), 2.iii.2000, 9 ♀♀, 5 ♂♂ (7 ♀♀, 4 ♂♂ visiting

yellow flowers of *Berkheya schinzii*; 2 ♀♀, 1 ♂ visiting yellow flowers of *Hirpicium echinus* Less., Asteraceae); Klein-Aus Vista (26.41S 16.13E), 23.ix.2003, 4 ♀♀, 3 ♂♂ (4 ♀♀, 2 ♂♂ (visiting yellow flowers of Asteraceae; 1 ♂ visiting yellow flowers of *Berkheya schinzii*); Aus (26.40S 16.15E), 2 and 3.iii.2000, 63 ♀♀, 30 ♂♂ (61 ♀♀, 29 ♂♂ visiting yellow flowers of *Berkheya schinzii*; 1 ♀, 1 ♂ visiting yellow flowers of *Dimorphotheca polyptera* DC., Asteraceae; 1 ♀ visiting white flowers of sp. of Aizoaceae: Mesembryanthema); Aus (26.40S 16.15E), 27.iv.1988 (C. D. Eardley), 32 ♀♀, 12 ♂♂ [NCP]; Sperrgebiet, Tsaukhaib (26.43S 15.40E), 13.ix.2005, 30 ♀♀, 7 ♂♂ (visiting yellow flowers of *Berkheya schinzii*); same locality, 14.ix.2005, 1 ♀ (visiting yellow flowers of *Tripteris sinuata* DC., Asteraceae); Sperrgebiet, E of Tsaukhaib (26.43S 15.42E), 13.ix.2005, 3 ♀♀ (visiting yellow flowers of *Berkheya schinzii*); Aus to Rosh Pinah (26.50S 16.18E), 11.ix.2003, 6 ♀♀, 4 ♂♂ (visiting yellow flowers of *Berkheya schinzii*); Namaskluft (27.52S 16.52E), 26.ix.2003, 1 ♂ (visiting yellow flowers of *Othonna* sp., Asteraceae); Namaskluft/Rosh Pinah (27.58S 16.46E), 12.ix.2003, 15 ♀♀ (visiting yellow flowers of *Tripteris microcarpa*); S of Rosh Pinah (27.58S 16.47E). 12.ix.2003, 11 ♀♀ (visiting yellow flowers of *Tripteris microcarpa*); 16 km S of Rosh Pinah (28.04S 16.51E), 13.x.2000, 58 ♀♀, 4 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*; same locality, 15.x.2000, 1 ♀; same locality, 12.ix.2003, 21 ♀♀, 5 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*); Karas Mountains, 6 km S on 201 from 26 (27.09S 19.01E), 7.iii.1999, 1 ♀ (visiting yellow flowers of *Vahlia capensis* (L.f.) Thunb., Vahliaceae); same locality, 5.iii.2000, 1 ♀ (visiting yellow flowers of *Geigeria ornativa* O. Hoffm., Asteraceae)–all F. W. and S. K. Gess [AMG] (unless otherwise indicated). SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Pootjiespram (28.05S 16.57E), 16.ix.1995 (F. W., S. K. and R. W. Gess), 3 ♀♀, 12 ♂♂ (1 ♀, 9 ♂♂ visiting yellow-rayed *Osteospermum* sp., Asteraceae; 1 ♂ visiting yellow flowers of *Cleome paxii* (Schinz) Gilg & Ben., Brassicaceae [formerly Capparaceae]; 2 ♂♂ visiting yellow flowers of *Didelta carnosa* (L. f.) Ait., Asteraceae; 2 ♀♀ visiting yellow flowers of *Grielum grandiflorum* (L.) Druce, Rosaceae); Richtersveld National Park, Koeroegabvlakte (28.11S 17.03E), 20.ix.1995 (F. W., S. K. and R. W. Gess), 1 ♀, 1 ♂ (on yellow flowers of *Osteospermum* sp.); Bushmanland, 24 km ENE of Aggeneys (29.08S 19.06E), 14.x.1988, 7 ♀♀ (on yellow daisy, Asteraceae); 22 km E of Williston on road to Carnarvon (31.16S 21.07E), 1.x.1989 (D. W. Gess), 1 ♀ (visiting flowers of *Gazania* sp., Asteraceae); 15 km N of Nieuwoudtville on road to Loeriesfontein (31.16S 19.08E), 7.x.1989, 1 ♀ (visiting flowers of *Senecio nivea* Less., Asteraceae); Nieuwoudtville Falls, 5 km N of Nieuwoudtville (31.19S 19.07E), 28.ix.1990, 1 ♀ (on yellow flowers of *Leysera gnaphaloides* (L.) L., Asteraceae); WESTERN CAPE: Prince Albert Dist., Tierberg (Study Site) (33.10S 22.16E), 5.xii.1987 (F. W., S. K. and R. W. Gess), 1 ♀ (on flowers of *Berkheya spinosa* (L.f.) Druce, Asteraceae); Molteno Pass nr. Beaufort West (32.12S 22.33E), 14.xii.1988 (C. D. Eardley), 2 ♀♀ [NCP]; Merweville (32.40S 21.30E), 15.xii.1988 (C. D. Eardley), 4 ♀♀ [NCP]–all F. W. and S. K. Gess [AMG] (unless otherwise indicated).

Geographic distribution.—Known in Namibia from the south-western part of the Mopane Savanna, the western part of the Semi-desert and Savanna Transition (Escarpment Zone), the Central Namib, and the eastern part of the Desert and Succulent Steppe of Giess (1971), and in South Africa from the Succulent Karoo and the western Nama Karoo.

Floral associations.—Very strongly associated with Asteraceae (*Berkheya, Didelta, Dimorphotheca, Emilia, Felicia, Gazania, Geigeria, Hirpicium, Leysera, Osteospermum, Othonna, Senecio,* and *Tripteris*), the few records of visits to the flowers of other plant families probably being incidental and of no account. In Namibia it is an expected visitor to *Tripteris microcarpa* wherever this plant occurs within its area of distribution and follows this plant along drainage channels across the Central Namib westwards to the coast.

Nesting.—Unknown.

Quartinia pteroniae Gess, new species

Diagnosis.—Small (2.5–2.7 mm long). Fore wing with Cu1a and 2*m-cu* thin, very pale to transparent. Tegula absolutely and evenly rounded posteriorly. Head, thorax and gaster black, shiny, with noticeable yellowish-white scutellar lamel-

lae, propodeal angles and posterior band on tergum I.

Description.—Female: Black. The following are light colored, ranging from yellowish-white (most markings on head and body) to reddish yellow (on antennae, legs and tegulae): mandible distally; underside of antenna; small spot at bottom of ocular sinus, small spot on gena behind top of eye, in a few specimens a minute spot on humeral angle and in some irregular and bilaterally asymmetrical narrow markings medially flanking hind margin of pronotum; in all specimens postero-dorsal angle of same; small spot at top of mesopleuron; tegula anteriorly and posteriorly (median part mid to dark testaceous); small spot postero-medially on scutellar disk; scutellar lamella (other than medially); propodeal angles; in all specimens an uninterrupted posterior band not reaching lateral margins on tergum I; in some specimens indications of posterior bands on one or more succeeding terga and in exceptional specimens with definite posterior bands on terga II–V; apex of femur, most of tibia and tarsomeres I–IV (becoming progressively darker) of all legs. Upper side of antennae reddish brown. Wings lightly darkened; veins brown.

Length 2.7 mm (average of 3); length of fore wing 1.8 mm (average of 3); hamuli 4.

Head in front view 1.23 × as wide as long (average of 3; range 1.22–1.25), microsculptured (shagreened), moderately shiny, with sparse, very shallow punctures. POL: OOL = 1: 0.78. Clypeus 1.6 × as wide as long; anterior margin shallowly emarginate; antero-lateral angles rounded.

Mesosoma microsculptured, moderately shiny, with punctures slightly larger and more noticeable than on head.

Gaster very finely microsculptured, shiny, with sparse, very small punctures.

Male. Black. The following are yellowish-white: mandible. underside of antenna; labrum, clypeus, transversely oval marking on lower half of frons (contiguous with white clypeus and centrally including a small dark brown spot); bottom of ocular sinus; streak on gena behind top of eye; uninterrupted narrow band flanking hind margin of pronotum and reaching postero-dorsal angle of same; large oval marking on humeral angle; large marking at top of mesopleuron; tegula anteriorly and posteriorly (median part mid testaceous); transverse marking postero-medially on scutellar disk; scutellar lamella (other than medially); propodeal angles; uninterrupted narrow posterior bands (slightly expanded medially and laterally) not reaching lateral margins of terga I–VI; apex of femur and most of tibia of all legs; first four tarsomeres of fore leg. Last tarsomere of fore leg and all tarsomeres of middle and hind legs brown. Upper side of antennae reddish brown. Wings lightly darkened; veins brown.

Length 2.5 mm.

Head in front view 1.34 × as wide as long. Clypeus 1.6 × as wide as long (measured to the bottom of the emargination); anterior margin widely and shallowly emarginate; antero-lateral angles rounded.

TergumVII slightly depressed posteriorly, narrowly and shallowly emarginate apically.

Sculpture and puncturation as in female.

Etymology.—The name *pteroniae*, genitive singular, is formed from the generic name of the plant *Pteronia pomonae* Merxm. (Asteraceae), on the capitula of which the wasp was most commonly found foraging for nectar or nectar and pollen.

Material examined.—Holotype ♀, NAMIBIA: Sperrgebiet, Klinghardtberge (27.14S 15.44E), 2.ix.2002 (F. W. and S. K. Gess) (visiting yellow flowers of *Pteronia pomonae* Merxm., Asteraceae) [AMG]. Paratypes: NAMIBIA: Sperrgebiet, Klinghardtberge (27.14S 15.43E), 1.ix.2002 (F. W. and S. K. Gess), 2 ♀♀ (visiting yellow flowers of *Pteronia pomonae*) [AMG]; Sperrgebiet, Klinghardtberge (27.14S 15.44E), 2.ix.2002 (F. W. and S. K. Gess) , 28 ♀♀, 2 ♂♂ (28 ♀♀, 1 ♂ visiting yellow flowers of *Pteronia pomonae*; 1 ♂ visiting flowers of *Rehlania* sp., Asteraceae)

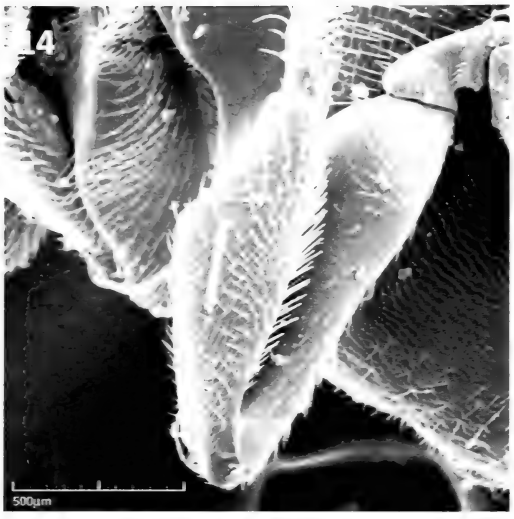


Fig. 14. *Quartinia pulawskii*, ♂, fore leg.

[AMG]; Sperrgebiet, Klinghardtberge (27.16S 15.45E), 3.ix.2002 (F. W. and S. K. Gess), 68 ♀♀ (all visiting yellow flowers of *Pteronia pomonae*) [AMG].

Geographic distribution.—Known from Namibia, from two localities in the west of the Desert and Succulent Steppe (Winter rainfall area) of Giess (1971).

Floral associations.—Found associated almost exclusively with *Pteronia pomonae* Merxm., Asteraceae).

Nesting.—Unknown.

Quartinia pulawskii Gess, new species (Fig. 14)

Diagnosis.—Small to medium sized (3.0–3.6 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins, and with 2*m-cu* interrupted before reaching M. Tegula rounded posteriorly. Male with femora and tibiae robust; fore tibia (Fig. 14) posteriorly excavate and narrowed in distal half; middle and hind femora antero-ventrally swollen.

Description.—Female: Black. The following are various shades of yellowish-white: underside of antenna (in part); bottom of ocular sinus; streak on temple behind upper part of eye; hind margin of pronotum (to postero-dorsal angle); large. diffuse area on humeral angle; streak at top of mesopleuron; anterior and posterior parts of tegula (median part testaceous); broad posterior band on disk of scutellum; scutellar lamella laterally; propodeal angle; posterior bands (expanded medially and laterally reaching or almost reaching sides) on terga I–V; posterior two-thirds of tergum VI; narrow posterior bands (in different specimens variously effaced) on sterna I–V; apex of femur, tibia and tarsomeres (latter progressively darkened; claws brown). Ferruginous are: distal half of mandible; upper side of antenna; margin of pale markings on mesosoma; anterior margin of pale posterior bands of terga; sterna (in part, particularly apical half of sternum VI). Wings sub-hyaline; veins brown.

Length 3.0–3.4 mm (average of 3: 3.3 mm); length of fore wing 2.1–2.4 mm (average of 3: 2.2 mm); hamuli 4.

Head in front view 1.2 × as wide as long; POL: OOL = 1: 0.7; clypeus 1.4 × as wide as long; anterior margin very shallowly emarginate; antero-lateral angles rounded.

Clypeus, frons and vertex almost matt, microsculptured (shagreened) with very indistinct, scattered, small punctures; mesonotum and scutellum moderately shiny, microsculptured, with distinct, scattered, small punctures; terga moderately shiny.

Male.–In coloration and markings similar to female but differing in the following respects: labrum varying from testaceous to yellowish-white; clypeus (other than for testaceous anterior margin and several small, diffuse, shadowy maculae, the most noticeable being a pair on lower half) and large sub-oval marking (including minute, dark, median spot) on lower half of frons and confluent (except for narrow black suture) with clypeus, yellowish-white; pale marking in ocular sinus larger.

Length 3.4–3.6 mm (average of 3: 3.5 mm; length of fore wing 2.2–2.4 mm (average of 3: 2.3 mm); hamuli 4.

Labrum inconspicuously carinate.

Tergum VII laterally obtusely angular, apically with a V-shaped incision, the lobes defining the latter sub-lamellate and narrowly rounded. Sternum II slightly swollen laterally; sternum VII depressed.

Femora and tibiae more robust than those of female; fore tibia (Fig. 14) posteriorly excavate and narrowed in distal half; middle and hind femora antero-ventrally swollen.

Etymology.—Named after Wojciech J. Pulawski of the California Academy of Sciences, collector of the present species and a much esteemed colleague and friend.

Material examined.—Holotype: ♂, NAMIBIA: Omaruru District, 20km NE Hentiesbaai (21°58'S 14°22'E), 10.xii.1996 (W. J. Pulawski) [CAS]. Paratypes: NAMIBIA: Omaruru District, 20km NE Hentiesbaai (21°58'S 14°22'E), 10.xii.1996 (W. J. Pulawski) 17 ♀♀, 29 ♂♂ [12 ♀♀, 24 ♂♂ CAS, 5 ♀♀, 5 ♂♂ AMG].

Geographic distribution.—Known only from a single locality in the Central Namib of Giess (1971).

Floral associations.—Not recorded.

Nesting.—Unknown.

Quartinia setosa Gess, new species

Diagnosis.—Small to medium sized (3.2–3.8 mm). Fore wing with Cu1a and 2*m-cu* present but attenuate, much thinner than other veins, and with 2*m-cu* interrupted before reaching M. Tegula rounded, with posterior inner corner angular but not inwardly produced. Both sexes predominantly black with yellowish-white markings and with noticeable, semi-erect, long, fine setae on terga.

Description.—Female: Black. The following are various shades of yellowish-white: underside of antennal club; narrow streak on temple behind upper part of eye; narrow anterior margin of pronotum and postero-dorsal angle of same, large humeral spot; tegula anteriorly and posteriorly (intermediate region testaceous); large spot anteriorly on mesopleuron; postero-medial marking on disk of scutellum; scutellar lamella laterally (area posterior to marking on disk dark); propodeal angle; narrow posterior bands, reaching sides, on terga I–V; very narrow posterior band on sternum IV; apex of femur, entire (or most of) tibia and all but ultimate tarsomere of all lega Reddish-brown are: mandibles (distally); scape, pedicel and intermediate flagellomeres; posterior margin of tergum VI. Wing membrane hyaline; veins brown.

Length 3.6–3.8 mm; length of fore wing 2.6–2.7 mm; hamuli 4–5.

Head in front view 1.28 × as wide as long, very finely microreticulate (shagreened), matt; clypeus apunctate; frons with inconspicuous small, shallow punctures separated by their width or less; vertex with punctures slightly larger and more definite than those of frons; POL: OOL = 1: 0.7. Clypeus 1.3 × as wide as long; anterior margin emarginate; anterolateral angles rounded. Mesosoma microreticulate with punctures larger and more obvious than those on head; punctures on mesonotum less closely set then those on pronotum; parapsidal furrows obvious. Gaster with terga noticeably setose.

Male: Black. Yellowish-white markings as in female, with in addition: mandibles (distally); labrum; disk of clypeus; pair of small spots on frons immediately above clypeo-frontal suture; distal half of tergum VII.

Length 3.2 mm; length of fore wing 2.0 mm; hamuli 4–5.

Structurally very similar to female and like it with noticeably setose terga.

Etymology.—The name *setosa* serves to draw attention to the unusually setose terga of both sexes.

Material examined.—Holotype: ♀, NAMIBIA: Sperrgebiet, S of Grillental on main north/south road (27.08S 15.25E), 9.ix.2005 (F. W. and S. K. Gess) (visiting yellow flowers of *Pteronia glabrata* L.f,, Asteraceae) [AMG]. Paratypes: NAMIBIA: same locality, date and collectors as holotype, 19 ♀, 2 ♂♂ (15 ♀♀, 2 ♂♂ visiting yellow flowers of *Pteronia glabrata* ; 3 ♀♀ visiting yellow flowers of *Pteronia pomonae* Merxm., Asteraceae;

1 ♀ visiting white flowers with pink flush of *Aridaria* sp., Aizoaceae: Mesembryanthema) [AMG].

Geographic distribution.—Known from Namibia, from a single locality in the west of the Desert and Succulent Steppe (Winter rainfall area) of Giess (1971).

Floral associations.—Almost exclusively found visiting the flowers of *Pteronia* species (Asteraceae); the only exception being one specimen visiting the flowers of *Aridaria* sp.(Aizoaceae: Mesembryanthema) which plant was growing next to the *Pteronia* plants.

Nesting.—Unknown.

Introduction to and discussion of the *tuberculifera* species group.
(Figs 15–17)

The following three species, *Q. tuberculifera*, *Q. tuberculiventris* and *Q. tuberculiventroides*, here associated as the *tuberculifera* species group, exhibit male secondary sexual characters which not only support a close relationship between them but also set them apart from all other species of *Quartinia*.

The first of these characters, as exemplified by *Q.tuberculiventris*, concerns the presence and the form of the tubercle on sternum I (Figs 15, 16). In itself the presence of a tubercle is by no means unique for, whereas not of universal occurrence, a tubercle of one form or another does occur in various species (for example *Q. conchicola* Gess, *Q. namaqua* Gess, *Q. obibensis* Gess and *Q. strucki* Gess); rather it is in its nature that the tubercle differs from those of other species. In all three species the tubercle is spout-like in shape, formed of the pronounced postero-ventrally directed production of the swollen sternum I, and extends beneath and beyond the base of sternum II. The near-truncate, slightly flared end of the tubercle (the "spout"), seen from behind, is semicircular, semi-oval to horseshoe-shaped in outline and is defined at least in part by a carina.

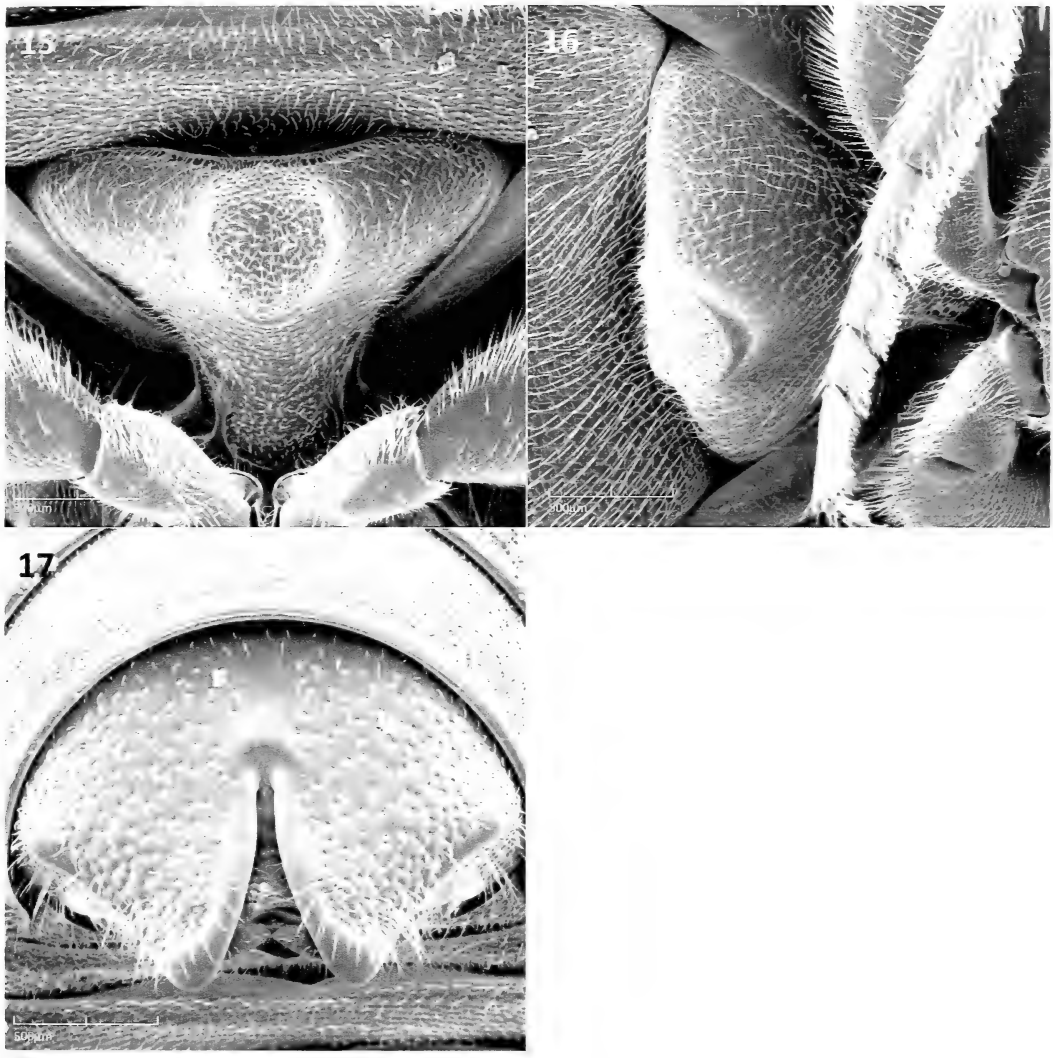
The second character, as exemplified by *Q. tuberculiventris*, concerns the form of tergum VII (Fig. 17). This is dorsally somewhat depressed medially, mid-laterally angularly produced, postero-medially deeply emarginate, and terminally with outwardly curving lobes roundly produced beyond the general apical curvature. A broad band margining the emargination and carried back onto the terminal lobes is smooth and contrasts markedly with the punctured and microsculptured surface of the rest of tergum.

All three species are readily distinguishable by their characteristic colour patterns which are remarkably consistent intraspecifically and divergent inter-specifically. This is particularly striking with respect to *Q. tuberculiventris* and *Q. tuberculiventroides* which have been found occurring sympatrically at several sites. Morphologically these two species differ in overall length (*Q. tuberculiventris* being in both sexes consistently larger), in setation (*Q. tuberculiventris* in both sexes having the clypeus, frons and vertex more obviously setose), and in the proportions of the clypeus (*Q. tuberculiventris* in both sexes having the width obviously less relative to the length).

The third species, *Q. tuberculifera*, apparently occurring allopatrically with respect to *Q.tuberculiventris* and *Q. tuberculiventroides* is morphologically distinguishable from both by the smaller malar space (× 0.4 of the width of the anterior ocellus as compared with × 0.8). Whereas this difference is common to both the males and females, it is more readily seen in the males on account of the pale integument of their "faces".

Quartinia tuberculifera Gess, new species
(Figs 18–20)

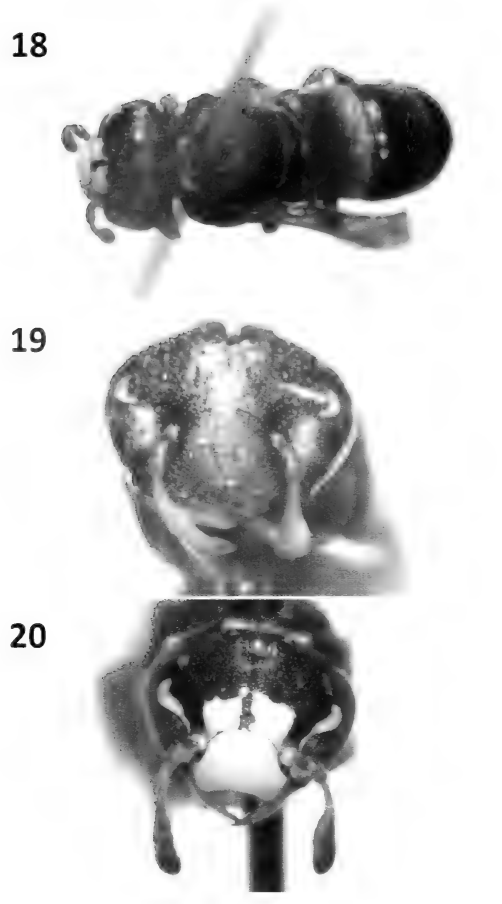
Diagnosis.—Medium sized (3.8–4.5 mm long). Fore wing with Cu1a and 2*m-cu* thin, the latter interrupted before reaching M. Tegula with posterior inner corner round-



Figs 15–17. *Quartinia tuberculiventris* ♂: 15, sternum I, postero-ventral view, showing tubercle; 16, sternum I, ventro-lateral view, showing tubercle; 17, tergum VII, dorsal view.

ed but somewhat inwardly produced; yellowish (except for dark testaceous discal spot). Male with spout-like tubercle on sternum I. Both sexes with malar space 0.4 × width of anterior ocellus (more readily seen in male than in female).

Description.—Female (Fig. 19): Black. The following are yellowish-white darkening to light ferruginous especially at margins of markings: streak behind eye on upper half of the gena (marking never produced onto vertex); narrow crescent-shaped marking at bottom of ocular sinus; in one specimen diffuse spots at clypeo-frontal suture and on sides of clypeus; underside of antennal club; humeral angle, hind margin (medially) and dorso-posterior angle of pronotum; potentially four longitudinal streaks posteriorly on mesoscutum, namely a medial pair in posteror third immediately anterior to scutellum (short, anteriorly wedge-shaped and pointed if present, in many specimens very reduced or totally absent) and a lateral pair flanking tegulae (present in only one specimen); in some specimens a small spot on axilla; tegula (except for



Figs 18–20. *Quartinia tuberculifera*: 18, ♂, dorsal view (× 12); 19, ♀, head, front view (× 26); 20, ♂, head, front view (× 26).

testaceous median region and lateral and posterior rim); disk of scutellum (except for convexly curved or bilobed baso-medial black marking; black in some specimens expanded and leaving only a small postero-medial pale mark); scutellar lamella; narrow oblique streak at top of mesopleuron; propodeal angles; terga I - VI (lightest in a narrow band across hind margins and progressively darkening anteriorly); streaks on distal half of femur of all legs, streaks on tibia of all legs.

Length 3.9–4.5 mm (average of 5 = 4.22 mm); length of fore wing 2.7 mm; hamuli 3.

Head in front view 1.26 × as wide as long (average of 3; range 1.24–1.28). POL: OOL = 1: 0.8. Clypeus 1.68 × as wide as long (average of 3; range 1.67–1.70). Frons and vertex not obviously setose (viewed tangentially to surface of integument) sparsely covered with short (length much shorter than diameter of ocellus), fine, semi-erect to erect, slightly curved setae. Pilosity on clypeus much denser than that on frons and vertex.

Frons and vertex somewhat shiny, only moderately closely punctured; punctures round bottomed, not noticeable reflective; interstices between the punctures of variable width but commonly equal to or exceeding puncture width, shagreened, noticeably reflective. Clypeus without punctures, matt, very finely shagreened.

Male (Figs 18, 20): Black. The following are yellowish-white darkening to light ferruginous especially at margins of markings: mandible (except base ventrally and teeth); labrum; clypeus; irregularly shaped pair of supraclypeal markings (occasionally fused) on lower half of frons; continuous marking from bottom of ocular sinus (where widened) down inner orbit (where narrow), across malar area, to bottom of gena (where produced around mandibular insertion and up lower part of occipital carina); streak behind top of eye; antenna (except progressively darkened dorsal aspect and almost totally dark last two flagellomeres); humeral angle, hind margin (medially) and dorso-posterior angle of pronotum; tegula (except for testaceous median region); small postero-median spot on scutellum and medially interrupted lamella of same; wedge-shaped marking at top of mesopleuron; propodeal angles (variously developed); ill-defined posterior bands on terga I–VI ; fore- and middle femora and tibiae predominantly; apex of hind femur and base and apex of hind tibia.

Length 3.8–4.2 mm (average of 6 = 4.0 mm); length of fore wing 2.7 mm.

Head in front view 1.27 × as wide as long (average of 3; range 1.24–1.31). POL: OOL = 1: 0.8. Clypeus 1.58 × as wide as

long (average of 3; range 1.56–1.61); malar space 0.4 × width of anterior ocellus.

Sternum I with its tubercle and tergum VII as described above for the *tuberculifera* species group.

Etymology.—The name, *tuberculifera*, meaning tubercle-bearing, draws attention to the tubercle on sternum I of the male.

Material examined.—Holotype ♂, NAMIBIA: Khorixas (15 km NW *(sic,* should read NE*)* of Twyfelfontein, Pad 2612) [20°32′49″ S, 14°24′02″ E], 24.xi.1994 (M. Kuhlmann) [Coll. M. Kuhlmann, London]. Paratypes: NAMIBIA: Khorixas (15 km NW *(sic,* should read NE*)* of Twyfelfontein, Pad 2612) [20°32′49″ S, 14°24′02″ E], 24.xi.1994 (M. Kuhlmann), 33 ♀♀, 6 ♂♂ [27 ♀♀, 4 ♂♂ Coll. M. Kuhlmann, London; 6 ♀♀, 2 ♂♂ AMG].

Geographic distribution.—Known from Namibia from a single locality in the Mopane Savanna of Giess (1971).

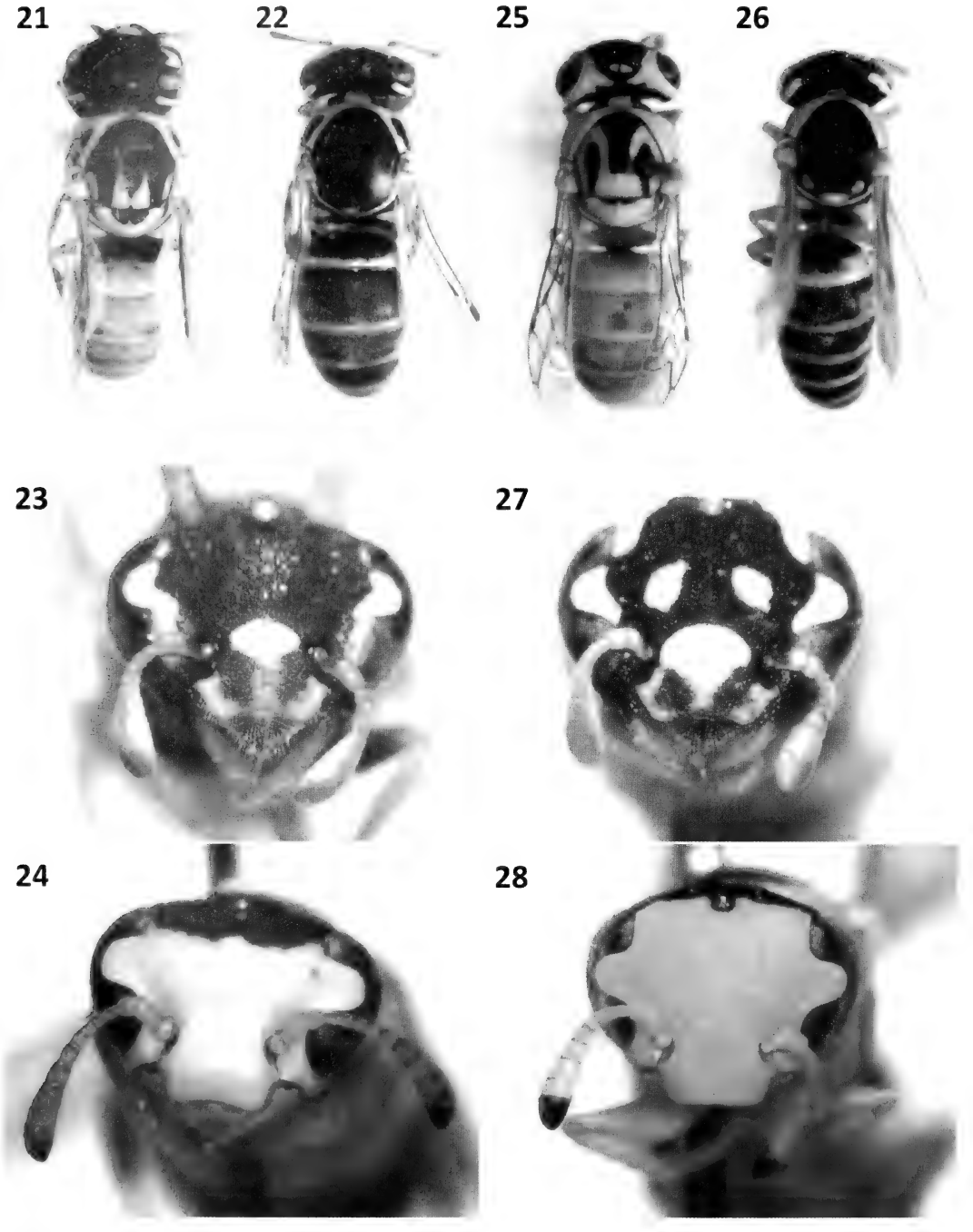
Floral associations.—Not recorded on data labels. In answer to a query with regard to the flowers on which the specimens were collected, Kuhlmann on 2 Nov. 2001 wrote that they were on a "blue Lamiaceae of 30-50 cm height". It is believed by the author and S. K. Gess that the plant was probably *Ocimum canum* Sims on which they have collected other Masarinae in Namibia.

Nesting.—Unknown.

Quartinia tuberculiventris Gess, new species
(Figs 15–17, 21–24)

Diagnosis.—Medium sized to large (3.9–5.0 mm long). Fore wing with Cu1a and 2*m-cu* thin, the latter interrupted before reaching M. Tegula with posterior inner corner markedly angular and somewhat inwardly produced, yellowish-white (except for pale testaceous discal spot). Male with spout-like tubercle on sternum I. Both sexes with malar space 0.8 × width of anterior ocellus (more readily seen in male than in female) with clypeus, frons and vertex obviously setose; streak behind eye on upper half of gena not produced onto vertex (nor in female produced down upper inner orbit); pale portion of "face" of male not rising laterally much above top of ocular sinus and medially at most just reaching median ocellus (in most specimens separated from median ocellus by at least one ocellar diameter if not more); mesonotum of female with lateral yellow marking (if present) short and in most specimens not exceeding anterior margin of tegula and with juxta-medial yellow marking short and wedge-shaped but, if produced, with anterior elongation very narrow and at most slightly outcurved apically; lateral and juxta-medial longitudinal markings of each side not meeting anteriorly in a smoothly rounded loop.

Description.—Female (Figs 21, 23): Black. The following are yellowish-white: in all specimens a streak behind eye on upper half of the gena (marking never produced onto vertex); in some specimens a variously developed crescent-shaped transverse band at bottom of gena above mandibular articulation; in a few specimens a very narrow band or series of minute spots along hind margin of eye, connecting or almost connecting above streak and transverse band (if present); in all specimens the ocular sinus; in a few specimens a narrow extension of sinus marking downwards along inner orbit to just above level of top of antennal socket, or two or more minute spots next to inner orbit at level of antennal socket, or a combination of the extension and the spots to form a narrow interrupted band along inner orbit; in a very few specimens minute isolated spots on the frons (medially immediately above the clypeus or next to the inner orbit above the sinus); markings on clypeus composed of a transverse basal band (exceptionally absent, or formed of irregular spots, or very narrow but entire, or lens-shaped, or trilobed, or triangularly produced towards anterior margin), broad lateral streaks or irregular spots below antennal sockets, and a narrow band (absent in some specimens) across anterior margin [in many specimens combining to form an anchor-shaped fig-



Figs 21–28. *Quartinia tuberculiventris*: 21, ♀, dorsal view (× 12); 22, ♂, dorsal view (× 12); 23, ♀, head, front view (× 26); 24, ♂, head, front view (× 26). *Quartinia tuberculiventroides*: : 25, ♀, dorsal view (× 12); 26, ♂, dorsal view (× 12); 27, ♀, head, front view (× 26); 28, ♂, head, front view (× 26).

ure or exceptionally, if very extensive, spreading over entire disk but for a pair of narrow oblique black streaks]; in many specimens two diffuse spots basally on labrum; underside of antennal club; hind margin and humeral angle of pronotum, or most of dorsal aspect of pronotum (with exception of broad and entire, or narrow and interrupted, or ill-defined and almost effaced lateral longitudinal streak), or entire dorsal aspect of pronotum; four longitudinal streaks posteriorly on mesoscutum, namely a medial pair in posteror third immediately anterior to scutellum (basally well separated, or touching, or broadly fused, anteriorly wedge-shaped and pointed, in some specimens very narrowly produced anteriorly over middle third of mesoscutum and terminally slightly outwardly curved and then together somewhat lyre-shaped) and a lateral pair flanking tegulae (in some specimens absent, in most specimens well developed and in one or two specimens anteriorly produced beyond level of postero-dorsal angle of pronotum); small spot on axilla; tegula (except for testaceous median region and lateral and posterior rim); disk of scutellum (except for convexly curved or bilobed baso-medial black marking); scutellar lamella; metanotum (in part); two or three markings on upper half of mesopleuron; dorsal aspect and lateral angles of propodeum; terga I–VI (except for lower half of anterior surface of tergum I and for faint transverse markings–brownish laterally on I–V and blackish medially on II–V); postero-medial part of sterna II–V and entire VI; a spot on mesocoxa (in some specimens); streaks on distal half of femur of all legs, tibiae of all legs; hind basitarsus [other tarsomeres progressively darkened distally].

Length 3.9–5.0 mm (average of 78: 4.3 mm); length of fore wing 3.2 mm; hamuli 4–5.

Head in front view 1.32 × as wide as long (average of 3; range 1.31–1.34). POL: OOL = 1: 0.8. Frons and vertex obviously setose (viewed tangentially to surface of integument), densely covered with moderately long (length approximating diameter of ocellus), moderately coarse, semi-erect to erect, slightly curved setae; very closely punctured; punctures flat bottomed, noticeably reflective in a circle around origin of seta; interstices in between punctures much narrower than puncture width, shagreened, only moderately reflective. Clypeus 1.5 × as wide as long (average of 3; range 1.46–1.52); pilosity as on frons and vertex; without punctures, shagreened.

Male (Figs 22, 24): Black. The following are various shades of yellow or yellowish-white: mandibles (except ferruginous tips), labium and maxillae; entire labrum and clypeus; most of frons (laterally to or slightly above level of top of ocular sinus and medially well separated from anterior ocellus or at most just reaching it); streak behind eye on upper half of gena (not produced onto vertex–that is not crossing an imaginary line drawn straight back from inner eye margin to occiput); in all specimens malar area and bottom of gena; in some specimens a very narrow band along hind margin of eye joining upper and lower genal markings; antennae (except for variously ferruginous flagellomeres in some specimens and black ultimate flagellomere in all specimens); most of pronotum (except transverse black streak at bottom of anterior face and in some specimens variously sized black lateral streak); in minority of specimens two or four poorly developed longitudinal streaks on mesoscutum, namely a medial pair (if present, barely indicated, or at most short, wedge-shaped and basally well separated) and a lateral pair flanking tegulae (if present, narrow) [in majority of specimens one or other pair or both pairs are totally absent]; in minority of specimens a small mark on axilla; tegula (except for testaceous median region and lateral and posterior rim); in all specimens a postero-medial spot on scutellar disk, in some anterolateral spots also, and in some

a fusion of the spots along hind margin; scutellar lamella; metanotum wholly or in part; at least anterior and lateral aspects of mesopleuron (in some specimens posterior aspect also); dorsal and lateral angles of propodeum; narrow transverse posterior bands (widened laterally on terga I–IV) on terga I–VI; sterna I–III or IV; coxa, trochanter, femur, tibia (except black streak on tibia of hind leg) and at least basitarsus (in most specimens) of all legs [other tarsi progressively darkened distally].

Length 4.1–5.0 mm (average of 23: 4.6 mm).

Head in front view 1.37 × as wide as long (average of 3; range 1.36–1.37). POL: OOL = 1: 0.8. Clypeus 1.42 × as wide as long (average of 3; range 1.40–1.43); malar space 0.8 × width of anterior ocellus.

Sternum I with its tubercle and tergum VII as described above for the *tuberculifera* species group.

Etymology.—The name *tuberculiventris*, denoting a tuberculate underside, draws attention to the tubercle on sternum I of the male.

Material examined.—Holotype: ♂, NAMIBIA: 113 km N[NW] of Swakopmund (21.51S 14.05E), 18.iii.2000 (F. W. and S. K. Gess) (visiting white flowers of *Brownanthus kuntzei* (Schinz) Ihlenf. and Bittrich, Aizoaceae: Mesembryanthema. Paratypes: NAMIBIA: 113 km N[NW] of Swakopmund (21.51S 14.05E), 18.iii.2000, 20 ♀♀, 8 ♂♂ (visiting white flowers of *Brownanthus kuntzei*); same locality, 21.iv.2002, 4 ♀♀, 3 ♂♂ (visiting white flowers of *Brownanthus kuntzei*); 110 km N[N]W of Swakopmund (21.50S 14.05E), 15.iii.1999, 39 ♀♀, 30 ♂♂(visiting white flowers of *Brownanthus kuntzei*); 10 km N of Swakopmund at wireless mast (22.35S 14.32E), 21.iii.1997, 39 ♀♀, 15 ♂♂ (2 ♀♀ visiting white flowers of *Psilocaulon salicornioides* (Pax) Schwantes, Aizoaceae: Mesembryanthema; 33 ♀♀, 12 ♂♂ visiting white flowers of *Brownanthus kuntzei*; 4 ♀♀, 3 ♂♂on ground); same locality, 11.iv.1998 1 ♂ (visiting white flowers of *Brownanthus kuntzei*); 97 km by road from Swakopmund to Usakos (22.10S, 15.10E), 16.iii.2000, 1 ♀ (visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae)–(all F.W. and S. K. Gess) [all AMG]; Swakopmund Dist., Rössing Mine (22.28S 15.02E), 1.iii.–10.iv.1984, 1 ♀; same locality, 31.vii.–28.viii.1984, 1 ♀; Upper Panner Gorge (22.29S 15.01E), 10.iv.–8.v.1984, 1 ♀; same locality, 23.x.–20..xi.1984, 1 ♀ - (all J. Irish; H. Liessner) [all NNIC].

Geographic distribution.—Known only from Namibia, from the seaboard and interior of the Central Namib of Giess (1971).

Floral associations.—Along the seaboard of the Central Namib almost exclusively associated with *Brownanthus kuntzei*; along drainage lines within the Central Namib found associated with *Zygophyllum simplex*.

Nesting.—Unknown.

Quartinia tuberculiventroides Gess, new species
(Figs 25–28)

Quartinioides sp. #1. (Wharton, 1980)

Diagnosis.—Small to medium sized (3.4–4.2 mm long). Fore wing with Cu1a and 2*m-cu* thin, the latter interrupted before reaching M. Tegula with posterior inner corner inwardly produced. Male with spout-like tubercle on sternum I. Both sexes with malar space 0.8 × width of anterior ocellus (more readily seen in male than in female); clypeus, frons and vertex not obviously setose; streak behind eye on upper half of gena produced onto vertex (and in female produced down upper inner orbit); pale portion of "face" of male rising laterally to near top of inner orbits and medially partially surrounding median ocellus and at least reaching posterior ocelli (which it may exceed); mesonotum of female with both lateral and juxta-medial yellow markings anteriorly produced, the anterior elongation of the latter wide; lateral and juxta-medial longitudinal markings of each side in almost all specimens meeting anteriorly in a smoothly rounded loop.

Description.—Female (Figs 25, 27): Black. The following are yellowish-white: in all specimens a streak behind eye on upper

half of the gena, produced onto the vertex behind top of eye [in most specimens markings of each side separate but in some specimens interruptedly connected by a number of irregular spots or joined to form a broad transverse band crossing the vertex behind the posterior ocelli] and with a ramus flanking the inner orbit produced down onto face on which in some specimens it reaches no further than to the top of the frons but in others extends down the frons as a broad band (occasionally interrupted and represented below by an isolated spot) to a level above or at top of ocular sinus and broadly separated, almost touching, or broadly fused with marking in sinus; in all specimens the ocular sinus; in some specimens two or more minute spots next to eye margin at level of antennal socket or marking in sinus downwardly produced as an unbroken band to this level or even to mandibular articulation; in some [but by no means all] specimens additional markings on the frons in the form of scattered irregular and bilaterally asymmetrical spots, or a fusion of spots on the lower half of frons to form an oval or an inverted Y, or a fusion and expansion of spots to form a broad, medially upwardly curved, transverse band broadly fused with markings in ocular sinuses and with bands flanking upper orbits (but excepting a small black area just outside ocular sinus), or an even greater expansion to cover entire frons (but excepting a black vertical streak below posterior ocellus, a small black area just outside ocular sinus, and black spots at the bottom of the frons, one medially and one above antennal socket); in some specimens a poorly developed crescent-shaped transverse band at bottom of gena above mandibular articulation; in a few specimens a very narrow band or series of minute spots along hind margin of eye, almost connecting streak at top of gena to transverse band at bottom; markings on clypeus composed of a transverse basal band (exceptionally absent, or formed of irregular spots, or very narrow but entire, or lens-shaped, or triangularly produced towards anterior margin), broad lateral streaks or irregular spots (absent in some specimens) below antennal sockets, and a narrow band (absent in some specimens) across anterior margin [in some specimens combining to form an anchor-shaped figure or exceptionally, if very extensive, spreading over entire disk but for a pair of narrow oblique black streaks; conversely, if melanistic, clypeus may be without any markings or may have only the transverse basal band]; in many specimens two diffuse spots basally on labrum; underside of antennal club entire; dorsal aspect of pronotum; four longitudinal streaks on mesoscutum, namely a medial pair broadly fused basally and a lateral pair flanking tegulae; medial and lateral streaks of each side broadly anteriorly produced and in all but very exceptional specimens meeting uninterruptedly in a smoothly rounded loop on anterior third of mesoscutum; most or all of axilla; tegula (except for testaceous median region and lateral and posterior rim); disk of scutellum (except for variously reduced to almost totally effaced bilobed baso-medial black marking); scutellar lamella; metanotum; upper half or more of mesopleuron; upper half or more of metapleuron; entire propodeum; terga I–VI (except in some specimens the very bottom of anterior surface of tergum I and in some specimens very faint brownish transverse markings laterally on terga II–V); diffuse postero-lateral and postero-medial markings on sterna II–V and entire VI; variously developed spots on coxae of all legs; trochanters (in part); distal half or more of femur of all legs, tibia of all legs; basitarsi of at least middle and hind legs [other tarsomeres progressively darkened distally].

Length 3.4–4.2 mm (average of 68: 3.7 mm); length of fore wing 2.6 mm; hamuli 4–5.

Head in front view 1.33 × as wide as long. POL: OOL = 1: 0.8.

Frons and vertex not obviously setose (viewed tangentially to surface of integument), densely covered with short (length much shorter than diameter of ocellus), fine, semi-erect to erect, slightly curved setae; very closely punctured; punctures non-reflective; interstices between punctures much narrower than puncture width, shagreened, only moderately reflective. Clypeus 1.65 × as wide as long (average of 3; range 1.63–1.68); pilosity as on frons and vertex; without punctures, shagreened.

Male (Figs 26, 28): Black. The following are various shades of yellow or yellowish-white: mandibles (except ferruginous tips), labium and maxillae; entire labrum, clypeus and frons; supra-facial portion of vertex to near top of inner orbits and at least to lower margin of posterior ocelli but in some specimens extending to behind posterior ocelli (leaving a transverse black area between them); streak behind eye on upper half of gena slightly produced onto vertex (that is crossing an imaginary line drawn straight back from inner eye margin to occiput) and, depending upon extent of supra-facial marking, broadly separated, almost touching or touching latter; in all specimens malar area and bottom of gena; in some specimens a narrow band along hind margin of eye joining upper and lower genal markings; antennae (except black last flagellomere); entire pronotum (except transverse black streak at bottom of anterior face); in majority of specimens two or four variously developed longitudinal streaks on mesoscutum, namely a medial pair (if present, barely indicated, or moderately developed but basally well separated, or well developed and basally broadly fused) and a lateral pair flanking tegulae (if present, moderately developed, or well developed); medial and lateral pair of streaks of each side, if well developed, broadly anteriorly produced and meeting uninterruptedly in a smoothly rounded loop on anterior third of mesoscutum; in some specimens most or all of axilla; tegula (except for testaceous median region and lateral and posterior rim); postero-medial spot or postero-medial and antero-lateral spots on disk of scutellum or entire scutellum (except for variously reduced to almost totally effaced bilobed baso-medial black marking); scutellar lamella; metanotum; entire mesopleuron; part of or entire metapleuron; entire propodeum (except pair of black markings on declivous face in darker specimens); transverse posterior bands (widened laterally on terga I–III) on terga I–VI in darker specimens; almost entire tergum I, greater part of terga II–VII (except base of II and apical half of VII and paired submedial and lateral spots on II–VI) in lighter specimens; sterna I–IV or V; coxa, trochanter, femur, tibia (except black streak on tibia of hind leg in some specimens) and at least basitarsus (in most specimens) of all legs [other tarsi progressively darkened distally].

Length 3.9–4.0 mm.

Head 1.29 × as wide as long (average of 3; range 1.28–1.33). POL: OOL = 1: 0.8. Clypeus 1.56 ×as wide as long (average of 3; range 1.53–1.59); malar space 0.8 × width of anterior ocellus.

Sternum I with its tubercle and tergum VII as described above for the *tuberculifera* species group.

Etymology.—The name, *tuberculiventroides*, serves to draw attention to the general similarity and relatedness of this species to *Q. tuberculiventris* and thereby to their shared possession of a tubercle on sternum I of the male.

Material examined.—Holotype: ♂, NAMIBIA: 33 km by road from Swakopmund to Usakos, near Rössing Mountain (22.34S, 14.49E), 15.iv.2002 (F. W. and S. K. Gess) (visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae) [AMG]. Paratypes: NAMIBIA: 110 km N[N]W of Swakopmund (21.50S 14.05E), 15.iii.1999, 69 ♀♀, 2 ♂♂ (28 ♀♀ visiting white flowers of *Brownanthus kuntzei* (Schinz) Ihlenf. and Bittrich, Aizoaceae: Mesembryanthema; 10 ♀♀, 2 ♂♂ visiting yellow flowers of *Tripteris microcarpa* Harv.[on labels as *Senecio* sp.], Aster-

aceae; 2 ♀♀ visiting yellow flowers of *Myxopappus hereroensis* (O.Hoffm.) Källersjö [on labels as "button" capitulae], Asteraceae; 29 ♀♀ visiting yellow flowers of *Galenia papulosa* (Eckl. and Zeyh.) Sond., Aizoaceae: non-Mesembryanthema); 10 km N of Swakopmund at wireless mast (22.35S 14.32E), 21.iii.1997, 11 ♀♀, 1 ♂ (1 ♀, 1 ♂ visiting white flowers of *Psilocaulon salicornioides* (Pax) Schwantes, Aizoaceae: Mesembryanthema; 2 ♀♀ visiting white flowers of *Brownanthus kuntzei*; 8 ♀♀ on ground); Swakop River bed on road to Goanikontes (22.41S 14.35E), 11.iv.1998, 3 ♀♀, 1 ♂ (visiting white flowers of *Psilocaulon salicornioides*); plains south of Goanikontes (22.42S 14.47E), 16.iv.2002, 19 ♀♀, 1 ♂ (16♀♀, 1♂ visiting pink flowers of ?*Leucosphaera bainsii* (Hook. F.) Gieg., Amaranthaceae; 1 ♀ visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae; 2 ♀♀ visiting white flowers of *Zygophyllum stapfii* Schinz); Rössing Mine (22.26S 15.03E), 22.iv. 2002, 2 ♀♀ (visiting white flowers of *Heliotropium tubulosum* E. Mey. ex DC., (Boraginaceae); 16.5 km by road from Swakopmund to Usakos (22.37S, 14.40E), 14.iii.2000, 17 ♀♀, 2 ♂♂ (visiting yellow flowers of *Tripteris microcarpa*) [on labels as yellow fls Asteraceae]; 33 km by road from Swakopmund to Usakos, near Rössing Mountain (22.34S, 14.49E), 15.iii.2000, 16 ♀♀ (14 ♀♀ visiting yellow flowers of *Tripteris microcarpa* [on labels as yellow fls Asteraceae]; 1 ♀ visiting white flowers of *Galenia africana* L.); same locality, 15.iv.2002, 27 ♀♀, 28 ♂♂ (2 ♀♀, 6 ♂♂ visiting yellow flowers of *Tripteris microcarpa* [on labels as *Osteospermum microcarpum*]; 9 ♀♀, 1 ♂ visiting white flowers of *Galenia africana*; 14 ♀♀, 19 ♂♂ visiting yellow flowers of *Zygophyllum simplex*; 1 ♂ visiting yellow flowers of Cucurbitaceae; 2 ♀♀ visiting pink flowers of *Indigophora* sp., Fabaceae: Papilionoideae); same locality, 28.iv.2002, 6 ♀♀, 4 ♂♂ (1 ♀ visiting yellow and orange flowers of *Adenolobus pechuelii* (Kuntze) Torre and Hillc., Fabaceae: Caesalpinoideae; 3 ♀♀, 1 ♂ visiting yellow flowers of *Tripteris microcarpa* [on labels as *Osteospermum microcarpum*]; 3 ♂♂ visiting yellow flowers of *Zygophyllum simplex*; 2 ♀♀ visiting white flowers of *Zygophyllum stapfii*); same locality, 31.iii.2004, 2 ♀♀ (1 ♀ visiting yellow flowers of *Tripteris microcarpa*.; 1 ♀ visiting yellow flowers of *Zygophyllum simplex*); 74 km by road from Swakopmund to Usakos (22.19S 15.06E), 15.iii.2000, 1 ♀ (visiting yellow flowers of *Tripteris microcarpa*); 97 km by road from Swakopmund to Usakos (22.10S, 15.10E), 16.iii.2000, 1 ♀ (visiting yellow flowers of *Zygophyllum simplex*)–(all F. W. and S. K. Gess) [all AMG]; Swakopmund Dist., Upper Ostrich Gorge (22.29S 14.59E), 13.iii.–10.iv.1984, 1 ♀, 1 ♂; Upper Panner Gorge (22.29S 15.01E), 10.iv.–8.v.1984, 1 ♂; same locality, 18.xii.1984–15.i.1985, 2 ♂♂–(all J. Irish; H. Liessner) [all NNIC]; 5 km N of Gobabeb [circa 23.34S 15.03E], 17.xii.1978 (Wharton), 1 ♀ (on *Zygophyllum simplex*) (= Wharton's *Quartinioides* sp.#1) [Gobabeb Research Station]; Namib Naukluft Park, Homeb [23.38S 15.11E], 23.i.1988 (R. Miller and L. Stange), 1 ♀ [FSCA].

Geographic distribution.—Known only from Namibia, from the seaboard and interior of the Central Namib of Giess (1971).

Floral associations.—Along the seaboard of the Central Namib chiefly associated with *Brownanthus kuntzei, Galenia papulosa* and *Tripteris microcarpa*; along drainage lines within the Central Namib chiefly associated with *Tripteris microcarpa, Zygophyllum simplex* and *Galenia africana*.

Nesting.—Unknown.

ADDENDUM TO SPECIES DESCRIBED IN GESS (2007)

Quartinia bonaespei Gess

Quartinia bonaespei Gess, 2007: 213, figs 1, 7, ♀, ♂. Holotype: ♂, South Africa: Western Cape: on coast 4 km north of Bloubergstrand (AMG).

Additional material examined: SOUTH AFRICA; WESTERN CAPE: Strandfontein (3418 BA) [34.04S 18.34E], 1.xi.1960 (F. Gess), 1 ♀ [SAM].

This is the Strandfontein between Muizenberg and Strand. The record is the first from False Bay.

Quartinia conchicola Gess

Quartinia conchicola Gess, 2007: 217, figs 2, 8, ♀, ♂. Holotype: ♂, South Africa: Western Cape: 12 km N of Vanrhynsdorp (AMG).

Additional material examined: SOUTH AFRICA: NORTHERN CAPE: Koingnaas Mines

(30.10S 17.14E), 12–17.ix.2007, 5 ♀♀, 1 ♂, 12–17.xi.2007, 2 ♀♀; ditto (30.22S 17.19E), 12–7.ix.2007, 1 ♀; ditto (30.22S 17.20E), 8–13. vii. 2007, 2 ♀♀, 12–17 .ix.2007, 1 ♀, 1 ♂. (all from pan traps.) (all C. Lyons *et al.*) [all AMG]. WESTERN CAPE: near Brand-se-Baai (31.27S 18.00E), 21–25.ix.2007 (from pan trap) (C. Lyons *et al.*), 1♀ [AMG].

The above records from localities at the Koingnaas Mines and from the mines near Brand-se-Baai fall within the known distribution of *Q. conchicola*. At Koingnaas specimens were obtained from pan traps during the months that these were operational, July, September and November; at Brand-se-Baai one specimen was obtained during September.

Quartinia vexillata Gess

Quartinia vexillata Gess, 2007: 225, figs 4, 12, ♀, ♂. Holotype ♂, South Africa: Northern Cape: 23 km S of Alexander Bay (AMG).

Additional material examined: NAMIBIA: Diamond Area 1 [= Sperrgebiet], no locality (28.25S 16.19E), 16–29.ix.1994 (E. Marais), 5 ♀♀ (Pres[ervation] pitf[all] traps) [NNIC]; Diamond Area 1 [= Sperrgebiet], Chamais (27.50S 15.43E), 16–29.1x.1994 (E. Marais), 1 ♀ (Pres[ervation] pitf[all] trap) [NNIC]. SOUTH AFRICA: NORTHERN CAPE: Koingnaas Mines (30.10S 17.14E), 12–17.ix.2007, 6 ♀♀, 1 ♂, 12–17.xi.2007, 1 ♀; ditto (30.12S 17.15E), 12–17.xi.2007, 1 ♀; ditto (30.18S 17.18E), 12–17.ix.2007, 1 ♀; ditto (30.21S 17.18E), 12–17.ix.2007, 1 ♂; ditto (30.22S 17.19E), 12–17.ix.2007, 5 ♀♀, 12–17.xi.2007, 1♀; ditto (30.22S 17.20E), 12–17.ix.2007, 1 ♀. (all from pan traps.) (all C. Lyons *et al.*) [all AMG]. WESTERN CAPE: near Brand-se-Baai (31.22S 17.55E), 14–18.vii.2007, 1 ♀, 21–25.ix.2007, 25 ♀♀, 6 ♂♂, 17–22.xi.2007, 50 ♀♀, 2 ♂♂; ditto (31.23S 17.56E), 21–25.ix.2007, 22 ♀♀, 4 ♂♂, 17–22.xi.2007, 19 ♀♀, 1 ♂; ditto (31.25S 17.58E), 21–25.ix.2007, 1 ♀, 2 ♂♂, 17–22.xi.2007, 1 ♀; ditto (31.29S 18.01E), 14–18.vii.2007, 2 ♀♀, 21–25.ix.2007, 10 ♀♀, 6 ♂♂, 17–22.xi.2007, 1 ♀. (all from pan traps) (all C. Lyons *et al.*) [all AMG].

The above records from localities at the Koingnaas Mines and from the mines near Brand-se-Baai establish a south ward extension of the hitherto known distribution of *Q. vexillata*. Previously the species was known no further south than 60 km N of Port Nolloth (28,47S 16.38E). Specimens were obtained from pan traps during the three months that these were operational, July, September and November. Though three females were obtained at Brand-se-Baai as early as July, most specimens were obtained during September and November (13 ♀♀, 2 ♂♂ and 3 ♀♀ respectively at Koingnaas and 58 ♀♀, 18 ♂♂ and 71 ♀♀, 3 ♂♂ respectively at Brand-se-Baai).

ACKNOWLEDGMENTS

The following individuals are thanked for much appreciated assistance as specified: Sarah Gess of the Albany Museum, Grahamstown, co-collector of most of the Albany Museum's *Quartinia* material, for thirty seven years of happy, productive and synergistic fieldwork, for valuable discussion and encouragement; David, Harold and Robert Gess for their enthusiastic field assistance while on various expeditions undertaken by myself and Sarah Gess during the period 1987–1996; Coleen Mannheimer of the National Herbarium of Namibia, Windhoek for her invitation to join the Herbarium party on their expeditions to the Sperrgebiet in 2002, 2003 and 2005 and also for her determination of voucher specimens of Namibian plants visited for pollen and nectar by masarines; Eugene Marais of the Namibian National Insect Collection, Windhoek, Connal Eardley of National Collection of Insects, Pretoria, Simon van Noort and Margie Cochrane of the South African Museum, Cape Town, Wojciech Pulawski of the California Academy of Sciences, San Francisco, Lionel Stange and Jim Wiley of the Florida State Collection of Arthropods, Gainesville, and Michael Kuhlmann, M. Kuhlmann Collection, London for the loan of specimens from their respective collections; Candice Lyons of the University of Cape Town for housing her *Quartinia* voucher material, derived from her study of the measure of success of restoration techniques on two strip-mining sites on the Namaqualand coast, in the Albany Museum and allowing me to use it and the associated data for my own purposes; Christine Taylor of the Natural History Museum, London for the loan of some *Quartinia* types; Shirley Pinchuck and Marvin Randall of the Electron Microscopy Unit of Rhodes University for help with the production of SEMs; Martin Hill of the Department of Zoology and Entomology of Rhodes University for allowing access to the photographic equipment in his laboratory and Tony Henningen of the same department for guidance in its use; and Bronwyn McLean of the Graphics

Services Unit of Rhodes University for help in the production of the figures.

Grateful thanks are expressed to those bodies which issued permits for the collection of insects and plant samples, namely: the Namibian Ministry of Environment and Tourism; the Namibian Ministry of Mines and Energy as also NAMDEB (Pty) Ltd (for the Sperrgebiet–Diamond Area No.1).

The South African Foundation for Research Development (FRD) and the South African National Research Foundation (NRF) are thanked for running expenses grants awarded to either myself and Sarah Gess or to Sarah Gess and myself for field work during the course of which much of the present material was collected. The Board of Trustees of the Albany Museum is thanked for Research Contracts granted to myself and Sarah Gess since 2003, which have given us continued use of the museum's facilities since our retirements.

LITERATURE CITED

André, Ed. 1884. *Spécies des Hyménoptères d'Europe et Algérie. Vol. 2.* Beaune, André and André.

Gess, F. W. 2007. The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part I. Description of new species with complete venation. *Journal of Hymenoptera Research* 16: 211–233.

———. 2008. The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part II. A new species with complete venation and with a deeply excised antennal club in the male. *Journal of Hymenoptera Research* 17: 83–85.

Gess, S. K. 1996. *The Pollen Wasps: Ecology and Natural History of the Masarinae*. Harvard University Press, Cambridge, Massachusetts, 340 pp.

——— and F. W. Gess. 1989. Flower visiting by masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae). *Annals of the Cape Provincial Museums (Natural History)* 18 5: 95–134.

——— and F. W. Gess. 2003. *A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa*. Grahamstown, Albany Museum, 529 pp.

Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4: 1–114.

Richards, O. W. 1962. *A revisional study of the masarid wasps (Hymenoptera: Masaridae)*. London. 294 pp.: British Museum (Natural History).

———. 1982. A new species of *Quartinioides* Richards (Hymenoptera, Masaridae). *Bullettino del Museo civico di storia naturale di Venezia* 32: 199–200. [1981].

Schulthess, A. von. 1930. Some more South African Masaridae (Vespoidea). *Annals and Magazine of Natural History* 5 10: 326–330.

——— and H. Scott. 1932. Some more South African Masaridae (Vespoidea), with notes on the mouthparts of the genera *Quartinia* and *Quartiniella*. *Annals and Magazine of Natural History* 10 10: 525–536.

Vecht, J. van der. and J. M. Carpenter. 1990. A catalogue of the genera of the Vespidae (Hymenoptera). *Zoologishe Verhandelingen* 260: 1–62.

Wharton, R. A. 1980. Insects and arachnids associated with *Zygophyllum simplex* (Zygophyllaceae) in the Central Namib Desert. *Madoqua* 12 3: 131–139.

J. HYM. RES.
Vol. 18(2), 2009, pp. 282–284

The Status of *Neivamyrmex goyahkla* and *Neivamyrmex ndeh* (Hymenoptera: Formicidae)

GORDON C. SNELLING AND STEFAN P. COVER

(GCS) 13161 Rancherias Road, Apple Valley, CA 92308, USA; email: myrmecophile@armyants.org
(SPC) Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA; email: scover@oeb.harvard.edu

Abstract.—The taxonomy of *Neivamyrmex* army ants (Hymenoptera: Formicidae) is complicated by the presence of species described from males only; for these taxa, the female castes remain unknown. Other *Neivamyrmex* species are known only from one or more female castes. Over time this has resulted in parallel systems of male and female-based names which cannot be reconciled until males and females are collected together in the field. The recent collection of a live dealate *Neivamyrmex* male and associated workers from a bivuoac in southern Arizona enables us to resolve one of these conundrums. Based on evidence provided by these specimens, *Neivamyrmex goyahkla* is here synonymized under *N. ndeh*.

When we described the army ants *Neivamyrmex goyahkla* and *Neivamyrmex ndeh* (Snelling and Snelling 2007) it was with the full realization that ultimately at least one of the species would probably be sunk into synonymy sometime in the future. However we did not anticipate that this would occur so soon after the paper was published. Thanks to a recent collection in Southern Arizona of a male specimen and associated workers by Stefan Cover and Lloyd Davis Jr., we can now reevaluate the status of these little-known species.

MATERIALS AND METHODS

Specimens utilized in the course of this study have been examined from the following:

Gordon C. Snelling, personal collection, Apple Valley, California, USA. (GCSC).

Natural History Museum of Los Angeles County, Los Angeles, California, USA. (LACM).

Museum of Comparative Zoology, Cambridge, Mass., USA. (MCZC).

SYSTEMATIC TREATMENT

Neivamyrmex ndeh Snelling and Snelling

Neivamyrmex ndeh Snelling and Snelling, 2007: 483. Holotype male, USA, Arizona, Santa Cruz Co., Yanks Canyon (B. V. Brown & D. Feener) (LACM) [examined].

Neivamyrmex goyahkla Snelling and Snelling, 2007: 470. Holotype worker, USA, Arizona, Santa Cruz Co., Ruby Road, 6.7 mi west of Hwy. I-19 (R. A. Johnson & G. C. Snelling) (LACM) [examined]. **NEW SYNONYMY**

New material examined: One wingless male and associated workers with the following collection data: USA Arizona Santa Cruz Co. Pajarito Mtns. 11.1 mi W Jct rte. 289 on FSR 89 31°27.51′ N 111°11.83′W 4300′ 14 VIII 2007 S. P. Cover and Lloyd Davis Jr. LD 140807-16 Open Mexican blue oak/Emory oak woodland to 20′ tall on rocky south facing slope under large rock in open. Coarse gravelly sand.

DISCUSSION

The male collected by Cover and Davis was discovered in a *Neivamyrmex*

colony whose workers clearly belong to *Neivamyrmex goyahkla*, a minute, shiny, orange species easily distinguished from similar congeners (*N. leonardi* and *N. nyensis*) by the presence of an antero-ventral tooth on the petiole. The male, however, is an excellent match for the holotype male of *N. ndeh*, a distinctive ant that is superficially similar to the male of *N. microps*, but from which it differs in important characters. *Neivamyrmex ndeh* is significantly smaller in size (HW 0.59 mm in *N. ndeh* vs HW 1.16 mm in *N. microps*) and has distinctive genitalic features: the presence of only two distinct teeth on the apical fork of the volsella, whereas three or more are present in *N. microps*.

Neivamyrmex goyahkla and *N. ndeh* belong to a group of inconspicuous, subterranean army ants with very small workers. As a result of their small size and subterranean habits, these *Neivamyrmex* are very infrequently collected, and the chances of finding males or queens with the workers are thus extraordinarily low. Unlike the workers, *Neivamyrmex* males are collected often, most commonly at lights and in Malaise traps. In the case of most Formicidae this would not present a problem, as unassociated males (i.e., males unassociated with workers) would not be described as new species without a very good reason. In contrast, unassociated army ant males have often been described as new species because of their bizarre appearance, relatively large size, and their considerable wealth of characters useful for identification purposes. Thus army ant taxonomy is complicated by the presence of a number of male-based taxa, for which the female castes remain unknown.

One solution to the problem of taxa based on males only is to ignore them, as E. O. Wilson chose to in his study of the Old World dorylines (Wilson 1964). Although the appeal of this approach is obvious, in our earlier paper on the *Neivamyrmex* of the United States (Snelling and Snelling 2007) we chose to follow the current trend of recognizing taxa based on unassociated males. Our reasoning was simply that the male taxonomic situation was so well established it would create more problems than it would solve to ignore taxa based on males only.

Even when working with males associated with workers, great care must be taken to assure that the association is real, not just accidental. This was made apparent to us during the course of the previous study when examining a male specimen taken in apparent association with *N. rugulosus*. We were quite excited by this, as the male of *rugulosus* is unknown. However, as we examined this specimen we became convinced that we were looking at a male of *N. harrisi*, a species common at the collection locality, and which had apparently stumbled into the *N. rugulosus* column by accident.

In this case of the specimen collected by Cover and Davis, however, circumstances surrounding the collection leave us confident the association between male and workers is real. According to the collection notes, the wingless male (males of army ants readily lose their wings when joining other colonies) was found alive and running among the workers during the excavation of the bivouac. This is strong evidence for conspecificity. In deciding which specific name to conserve we decided to retain the name that was both easiest to spell and pronounce. Therefore we have decided to synonymize *N. goyahkla* and retain *N. ndeh* as the valid name for this ant. No doubt, Roy would probably have argued that we retain *N. goyahkla* simply out of sheer orneriness.

ACKNOWLEDGMENTS

I (GCS) want to thank my father, Roy R. Snelling, to whom this paper is dedicated, for his support and extreme patience as I fumbled my way thru the learning curve that is Myrmecology. SPC wishes to thank Roy for being such a good friend for so long -

and for being an amazing source of myrmecological wisdom and teller of great stories.

LITERATURE CITED

Snelling, G. C. and R. R. Snelling. 2007. New synonymy, new species, new keys to *Neivamyrmex* army ants of the United States. 459–550 *in* Snelling, R. R., B. L. Fisher, and P. S. Ward, eds. *Advances in Ant Systematics (Hymenoptera: Formicidae: Homage to E. O. Wilson—50 years of contributions. Memoirs of the American Entomological Institute* 80: 459–550.

Wilson, E. O. 1964. The true army ants of the Indo-Australian area (Hymenoptera: Formicidae: Dorylinae). *Pacific Insects* 6: 427–483.

J. HYM. RES.
Vol. 18(2), 2009, pp. 285–304

The Ant Genus *Tetraponera* in the Afrotropical region: the *T. grandidieri* group (Hymenoptera: Formicidae)

PHILIP S. WARD

Department of Entomology, University of California, Davis, CA 95616, USA

Abstract.—Ants in the *Tetraponera grandidieri* group are endemic to the island of Madagascar, where they occur in relatively undisturbed mesic forest. In this taxonomic revision of the group seven species are recognized: *T. grandidieri* (Forel), *T. hespera* **sp. n.**, *T. hirsuta* **sp. n.**, *T. inermis* **sp. n.**, *T. manangotra* **sp. n.**, *T. merita* **sp. n.** and *T. variegata* (Forel) **stat. n.** *T. grandidieri hildebrandti* (Forel) is proposed as a new synonym of *T. grandidieri*. The species in this group show limited morphological and genetic divergence. The justification for treating them as different species is that they occur sympatrically in various combinations, without showing genetic or phenotypic intergradation. Although differences in shape, pilosity and sculpture are not pronounced, there is notable color pattern variation, both within and among species. The conspicuous orange and reddish-brown color that characterizes the workers and queens likely serves as warning coloration. These ants have painful stings and several species of ants in the *Camponotus putatus* complex exhibit color patterns that apparently mimic those of the *T. grandidieri* group.

Twig-dwelling ants in the subfamily Pseudomyrmecinae are a distinctive component of the arboreal ant fauna in forests and woodlands of both the Neotropics and Paleotropics (Ward and Downie 2005). The Afrotropical representatives of the subfamily, currently placed in the genus *Tetraponera* F. Smith, were recently divided into five monophyletic species groups (Ward 2006). Four of the five groups occur in Madagascar and one of these, the *Tetraponera grandidieri* group, is endemic to the island. The group has never received the benefit of a modern taxonomic treatment. There is only a single named species, *T. grandidieri* (Forel), with two nominal subspecies, but the current study reveals substantially greater species-level diversity, paralleling the situation for the ant fauna of Madagascar as a whole, where considerable numbers of species remain undescribed (Fisher 2003). Species are here delimited using a combination of morphological, geographical and genetic evidence, while working within the framework of the biological species concept (Mayr 1963; Coyne and Orr 2004).

This paper is dedicated to the memory of Roy Snelling, a colleague, friend and ardent hymenopterist. In his later years Roy developed an interest in the ant fauna of the Afrotropical region, specifically that of Kenya, and his last days were spent there. Roy's generosity, candor, pungent humor, and enthusiasm for ants and other aculeate Hymenoptera left an indelible impression on those who had the pleasure of interacting with him.

MATERIALS AND METHODS

Specimens were examined in the following collections:

BMNH	Natural History Museum, London, UK
CASC	California Academy of Sciences, San Francisco, CA, USA
CUIC	Cornell University Insect Collection, Ithaca, NY, USA
MCSN	Museo Civico de Historia Natural "Giacomo Doria", Genoa, Italy

MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMV	Naturhistorisches Museum, Vienna, Austria
PSWC	P. S. Ward Collection, University of California at Davis, CA, USA
SAMC	South African Museum, Cape Town, South Africa
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, USA
USNM	National Museum of Natural History, Washington, DC, USA

Standard measurements (in mm) and setal counts were taken at 50× with a Wild M5A microscope, as described in Ward (2001, 2006). The abbreviations used for measurements, indices and setal counts are given below. The first four measurements are taken with the head in full-face view, such that the posterior margin of the head and the anterolateral corners are in the same plane of view.

HW	Maximum head width, including eyes.
HL	Head length, taken along the midline, from the posterior margin of the head to the anterior extremity of the clypeus.
EL	Eye length, measured in the same plane of view as HL.
MFC	Minimum distance between the frontal carinae.
SL	Scape length, excluding the radicle.
FL	Length of profemur, measured along its long axis in posterior view.
FW	Maximum width of profemur, measured in the same view as FL and at right angles to it.
PL	Length of the petiole in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole.
PH	Maximum height of petiole, measured in the same view as PL, and excluding protruding teeth or lobes at the anteroventral or posteroventral extremities of the petiole.
DPW	Maximum width of petiole, measured in dorsal view.
LHT	Length of the metatibia, excluding the proximomedial condyle (Ward 2001, fig. 5).
CI	Cephalic index: HW/HL
FCI	Frontal carina index: MFC/HW
REL	Relative eye length: EL/HL
REL2	Relative eye length, using HW: EL/HW
SI	Scape index: SL/HW
FI	Profemur index: FW/FL
PLI	Petiole length index: PH/PL
PWI	Petiole width index: DPW/PL
CSC	Cepalic setal count: number of standing hairs (those forming an angle of 45° or more with the cuticular surface) visible on the posterior half of the head, as seen in lateral and posterior views
MSC	Mesosomal setal count: number of standing hairs visible in profile (lateral view) on the mesosoma dorsum

Automontage images of selected specimens (Figs 7–22) were taken by April Nobile and Erin Prado at the California Academy of Sciences (CAS), under the direction of Brian Fisher. These images are also posted on AntWeb (www.antweb.org), together with photographs of the type specimens of *T. grandidieri*, *T. grandidieri hildebrandti* (Forel) and *T. grandidieri variegata* (Forel).

The species described here were sequenced for fragments of one mitochondrial gene (COI) and several nuclear genes, using methods described in Ward and Downie (2005) and Brady et al. (2006). This molecular work is ongoing and results will be analyzed and presented in more detail elsewhere. The DNA sequence data provide ancillary information that helps to validate species boundaries inferred from morphology and geography.

Species distributions were plotted with the shareware program Versamap (Version 3.01). For most specimens examined in this study the coordinates (latitude and longitude) were given on the specimen label. For material lacking this information the following sources were used to georeference collection sites: Forel (1892), United States Board on Geographic Names (1989), Viette (1991), Huber (2003), the GEOnet Names Server (http://earth-info.nga.mil/gns/html/index.html), the Gazetteer to Malagasy Botanical Collecting Localities (http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/), and topographic maps of Madagascar at scales of 1:50,000, 1:100,000 and 1:500,000, published by Foiben-Taosarintanin' i Madagasikara (Institut Géographique et Hydrographique National). In the lists of material examined, most locality names are given verbatim from the specimen label, but in a few instances they have been interpreted for clarity. In this case the original spelling is given in quotes after the emendation (e.g., Anosibe An'ala [as "Nosibé, Village de l'Imerina"]). The abbreviation "c.u." signifies collector unknown.

RESULTS

Diagnosis of the *Tetraponera grandidieri* group
(modified from Ward 2006)

Worker diagnosis. Medium to large species (HW 0.95–1.59, HL 1.05–2.01, LHT 1.05–1.83); masticatory margin of mandible with four teeth; basal margin with 0–1 teeth and subequal in length to masticatory margin; labrum with a pair of tubercles closely flanking the midline near the proximal margin but lacking a median tubercle; palp formula 6,4; anteromedial margin of clypeus crenulate or emarginate; distance between frontal carinae exceeding basal scape width (FCI 0.11–0.18), scape length three-quarters or more of head width (SI 0.72–0.83); eye length about one-third of head length (REL 0.28–0.36); head capsule with three distinct ocelli; pronotum laterally marginate, but not strongly so; mesopropodeal impression well developed (Figs 5, 6); petiole relatively long (PLI 0.49–0.59, PWI 0.40–0.65); posteroventral margin of petiole lying adjacent to helcium venter; metabasitarsal sulcus present; legs long and slender (FI 0.28–0.36, LHT/HL 0.85–1.12); appressed pubescence sparse on abdominal tergite 4; standing pilosity uncommon (CSC 2-3, MSC 1-6), absent from mesonotum, propodeum, and extensor surfaces of the tibiae. Orange to reddish-brown, head concolorous or darker; gaster and portions of femora may also be infuscated.

Comments. Distinctive features of the worker caste of the *T. grandidieri* group include the relatively large body size, long legs and antennal scapes, presence of three ocelli, deeply impressed mesopropodeal impression, and conspicuous orange to reddish-brown body coloration. Other Malagasy *Tetraponera* species have shorter scapes and legs (SI 0.40–0.70, LHT/HL 0.58–0.82), 0–2 ocelli on the head, a shallower mesopropodeal impression, and usually darker body color. Additional differences between the *T. grandidieri* group and the other four species groups of Afrotropical *Tetraponera* are given in Ward (2006).

Synonymic list of species

T. grandidieri (Forel 1891: 203)

= *T. grandidieri hildebrandti* (Forel 1891: 203) **syn. n.**

T. hespera **sp. n.**
T. hirsuta **sp. n.**
T. inermis **sp. n.**
T. manangotra **sp. n.**
T. merita **sp. n.**
T. variegata (Forel 1895: 487) **stat. n.**

KEY TO SPECIES BASED ON THE WORKER CASTE

1 Basal margin of mandible with a prominent tooth, in addition to four teeth on the masticatory margin (Fig. 1); anterior clypeal margin deflected ventrally; widespread in eastern and northern Madagascar ..... ***merita***

– Basal margin of mandible lacking tooth, masticatory margin with four teeth (Fig. 2); anterior clypeal margin directed forward, not deflected ventrally 2

2(1) Petiole broad (PWI 0.61–0.65, DPW/HW 0.50–0.53), subtriangular in dorsal view, and with a relatively short, thick anterior peduncle (Fig. 20); larger species, HW 1.48–1.58, LHT 1.64–1.76; known only from extreme southern Madagascar ..... ***manangotra***

– Petiole more slender (PWI 0.40–0.53, DPW/HW 0.30–0.40), obovate, and with a thin, elongate anterior peduncle (e.g., Figs 14, 16, 18); smaller species, HW 0.95–1.44, LHT 1.05–1.59; widespread 3

3(2) Scape with conspicuous suberect and subdecumbent hairs (Fig. 13); body tricolored: metasoma, appendages, and ventral margin of mesosoma orange, most of mesosoma reddish-brown, and head dark brownish black; endemic to Manongarivo Massif .... ***hirsuta***

– Most hairs on scape appressed or decumbent, and generally inconspicuous, except those at the apex (e.g., Fig. 9); body color variable but usually without preceding tricolor pattern 4

4(3) Metanotal spiracle not protruding above the profile of the mesosoma, as seen in lateral view (Fig. 5); head broad (CI 0.88–0.97); head and mesosoma reddish-brown, metasoma and appendages paler; widespread in eastern Madagascar ..... ***inermis***

– Metanotal spiracle more or less protruding above the profile of the mesosoma, as seen in lateral view (Fig. 6); head usually more elongate (CI 0.77–0.90); color variable 5

5(4) Dorsum of propodeum laterally compressed, the propodeum appearing subtriangular in posterior view (Fig. 3); body concolorous orange-brown; northern Madagascar ..... ***hespera***, in part (Ankarana population)

– Dorsum of propodeum more broadly rounded, the propodeum appearing dome-shaped in posterior view (Fig. 4); color variable 6

6(5) Legs uniformly light orange-brown, femora lacking conspicuous black banding; body usually bicolored, such that dark head contrasts with lighter orange-brown mesosoma and metasoma (Fig. 8), less commonly unicolorous orange; widespread and variable species ..... ***grandidieri***

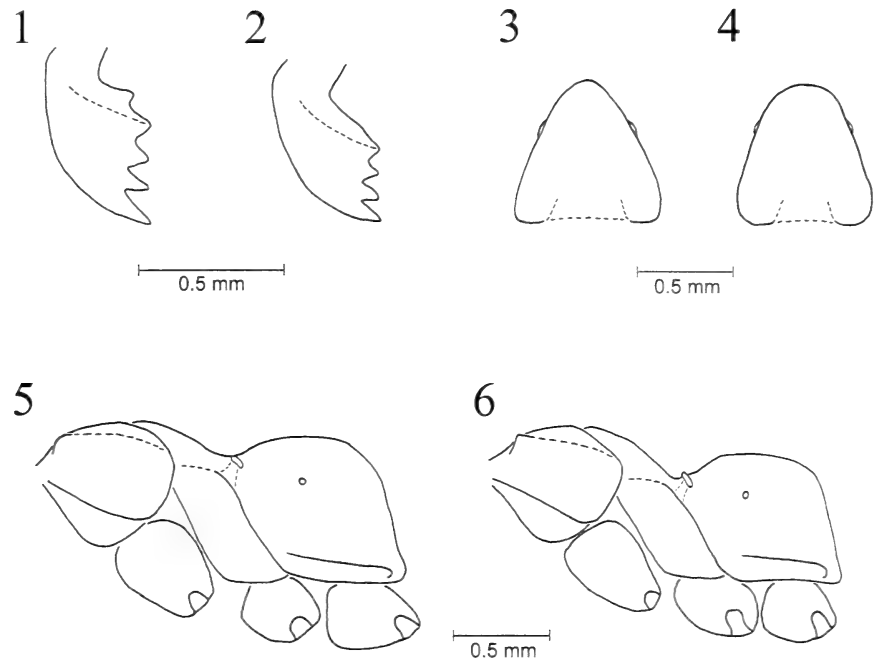
– Legs light orange-brown, with contrasting black bands on the distal portions of the mesofemur and metafemur (Figs 10, 22); body concolorous or bicolored (in latter case both head and gaster are dark brownish-black) 7

7(6) Body concolorous yellow brown or orange brown (Fig. 10); northwestern Madagascar ..... ***hespera***, in part (most populations)

– Body bicolored, head and gaster dark brown and contrasting with the lighter mesosoma (Fig. 22); eastern Madagascar ..... ***variegata***

Tetraponera grandidieri (Forel 1891)
(Figs 7–8, 19)

Sima Grandidieri Forel 1891: 203. Syntypes, 4 workers, Central Madagascar (Hildebrandt) (MCSN, MHNG) [examined] [Two of three MHNG syntypes imaged on AntWeb: CASENT0101652, CASENT0102029]. One syntype (CASENT0101652) here designated **lectotype**.



Figs 1–6. Workers of the *Tetraponera grandidieri* group, right mandible (1, 2), posterior view of propodeum (3, 4), and lateral view of mesosoma (5, 6). 1, *T. merita*; 2, *T. hespera*; 3, *T. hespera*, Ankarana population; 4, *T. hespera*, Nosy Bé; 5, *T. inermis*; 6, *T. hespera*.

Sima Grandidieri var. *Hildebrandti* Forel 1891: 204. Holotype (by monotypy) worker, Pays de Betsileo, "Sud Central Madagascar" (Hildebrandt) (MHNG) [examined] [Imaged on AntWeb: CASENT0101883]. **Syn. n.**

Sima grandidieri Forel; Forel 1891: 229–230. Description of queen and male.

Tetraponera grandidieri (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

Tetraponera grandidieri var. *hildebrandti* (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

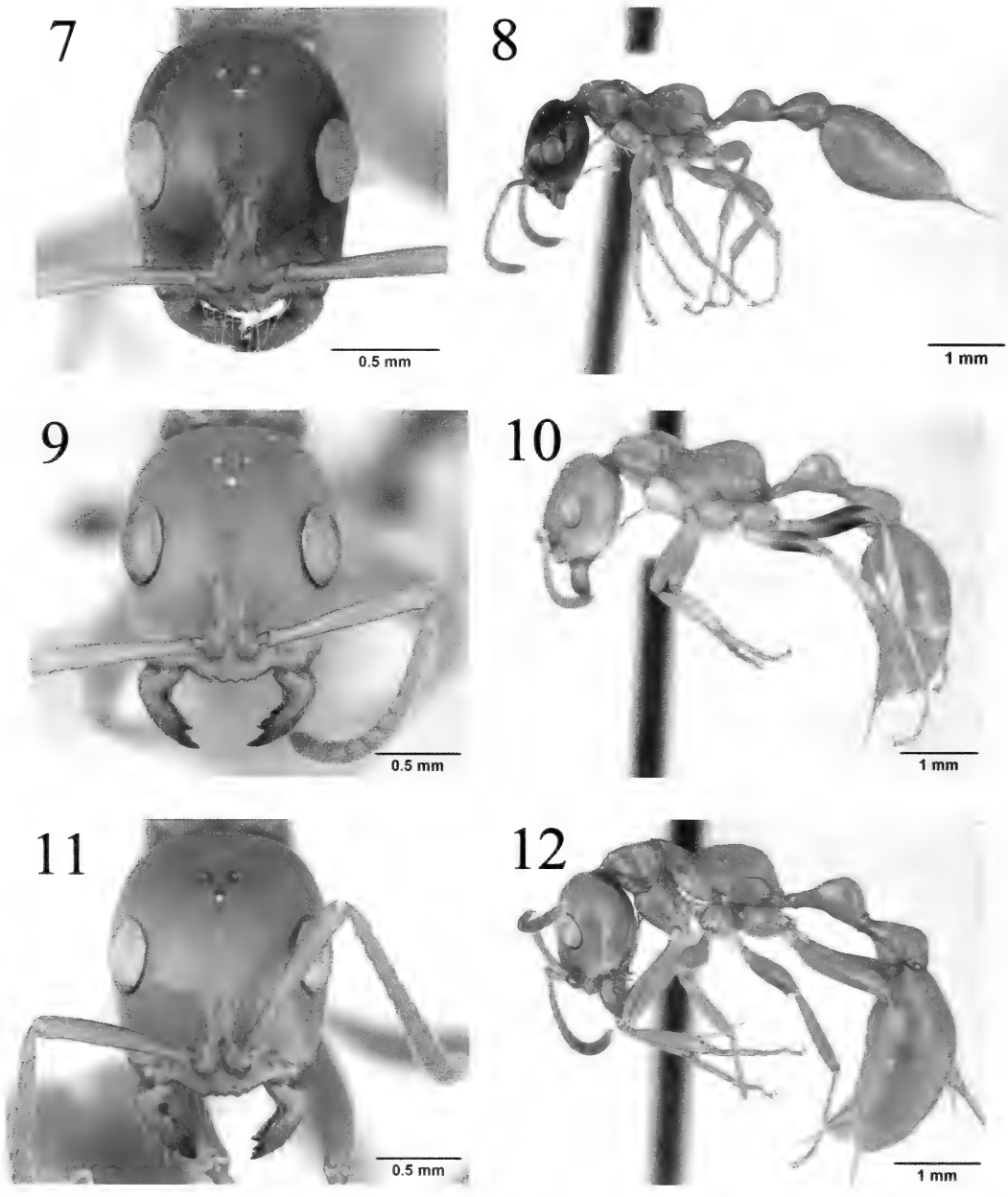
Tetraponera grandidieri (Forel); Ward, 1991: 342. Nesting biology.

Tetraponera grandidieri (Forel); Fisher 1996: 100; Fisher 1999: 134; Fisher 2002: 318. Cited in faunal inventories.

Tetraponera cf. *grandidieri* (Forel); Fisher 1998: 49. Cited in faunal inventory.

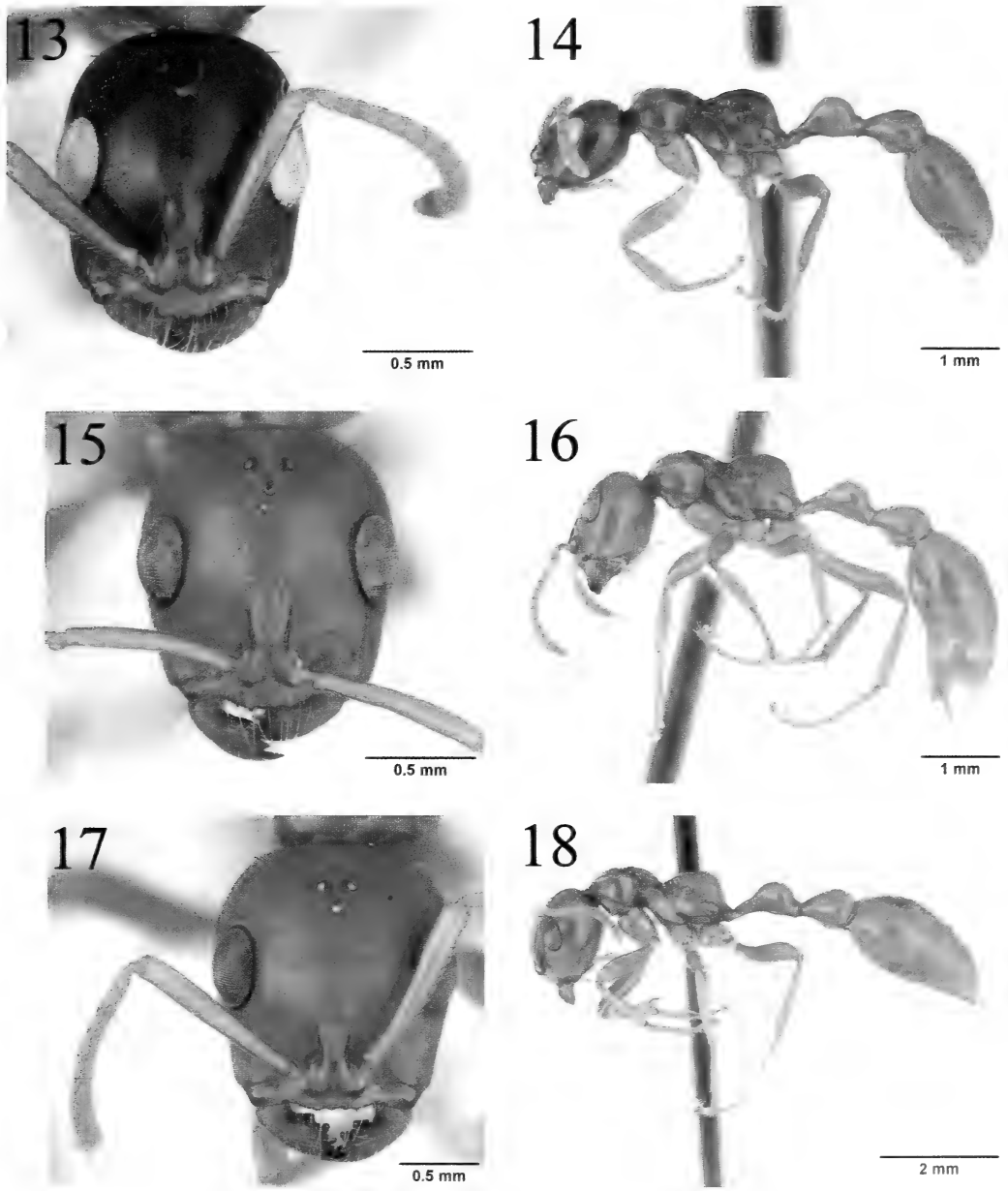
Tetraponera grandidieri (Forel); Ward and Downie 2005. DNA sequences of five nuclear genes; GenBank accession numbers AY703507 (18S rDNA), AY703574 (28S rDNA), AY703641 (wingless), AY703775 (long wavelength rhodopsin), and AY703778 (abdominal-A).

Material Examined.—(BMNH, CASC, MCSN, MCZC, MHNG, MNHN, NHMB, NHMV, PSWC, SAMC, UCDC, USNM) MADAGASCAR *Antananarivo*: Andrangoloaka (Sikora); *Antsiranana*: Montagne d'Ambre [?] [as "Amber geb."] (Rolle); 1 km W Andampibe, Cap Masoala, 125 m (Alpert, G. D.); 3 km W Andampibe, Cap Masoala, 125 m (Alpert, G. D.); 3 km W Sakalava Beach, 40 m (Schlinger; et al.); 4 km SW Ambohitra (=Joffreville), 1000 m (Ward, P. S.); 5 km SW Ambohitra (=Joffreville), 1100 m (Ward, P. S.); 7 km N Joffreville, 360 m (Harin'Hala, R.); Betaolana forest, 880 m (Fisher, B. L.; et al.); Diego Suarez (Alluaud, C.); Forêt Ambanitaza, 26.1 km 347° [NNW] Antalaha, 240 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.; et al.); Forêt Binara, 9.4 km 235° SW Dairana, 1100 m (Fisher, B. L.; et al.); Fotodriana, Cap Masoala, 25 m (Alpert, G. D.; et al.); Fotodriana, Cap Masoala, 25 m (Alpert, G. D.); Marojejy R.N.I., #12, 375 m (Alpert, G. D.); Marojejy R.N.I., #12, 665 m (DiRosa, R.); Montagne d'Ambre, 900 m (Alpert, G.; et al.); Montagne d'Ambre, Petit Lac, 1000 m (Alpert, G.; et al.); Montagne Français, 150 m (Harin'Hala, R.); P.N. Marojejy,



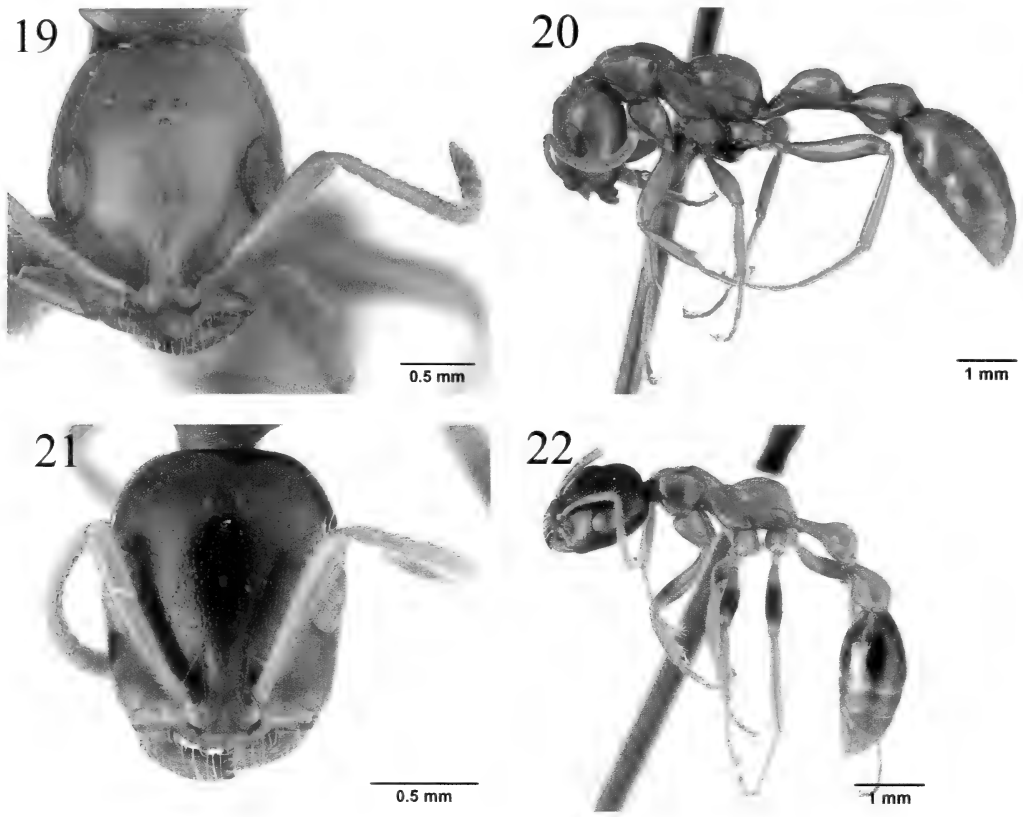
Figs 7–12. Automontage images of workers of the *Tetraponera grandidieri* group, full-face (dorsal) view of head (7, 9, 11) and lateral view of body (8, 10, 12). 7, 8, *T. grandidieri* (CASENT0012861); 9, 10, *T. hespera*, holotype (CASENT0012865); 11, 12, *T. hespera*, Ankarana population (CASENT0012864).

26.6 km 31° NE Andapa, 1325 m (Fisher, B. L.; et al.); P.N. Marojejy, 27.6 km 35° NE Andapa, 775 m (Fisher, B. L.; et al.); P.N. Marojejy, 28.0 km 38° NE Andapa, 450 m (Fisher, B. L.; et al.); P.N. Montagne Ambre, 1125 m (Harin'Hala, R.); P.N. Montagne Ambre, 3.6 km 235° SW Joffreville, 925 m (Fisher, B. L.; et al.); P.N. Montagne Ambre, 960 m (Harin'Hala, R.); P.N. Montagne Ambre, 960 m (Irwin, M. E.; et al.); P.N. Montagne Ambre, 960 m (Schlinger; et al.); P.N. Montagne Ambre, 975 m (Irwin, M. E.; et al.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3000 ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3200



Figs 13–18. Automontage images of workers of the *Tetraponera grandidieri* group, full-face (dorsal) view of head (13, 15, 17) and lateral view of body (14, 16, 18). 13, 14, *T. hirsuta*, holotype (CASENT0170370); 15, 16, *T. inermis*, holotype (CASENT0012862); 17, 18, *T. merita*, holotype (CASENT0012863).

ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3600 ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre, 1000–1100 m (Brown, W. L.; Brown, D. E.); Parc Nat. Montagne d'Ambre, 1100 m (Olson, D. M.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m (Fisher, B. L.); R.S. Manongarivo, 14.5 km 220° SW Antanambao, 1175 m (Fisher, B. L.); Réserve Spéciale Ambre, 3.5 km 235° SW Sakaramy, 325 m (Fisher, B. L.; et al.); Sakalava Beach, 10 m (Harin'Hala, R.); *Fianarantsoa*: 3 km W Ranomafana, nr. Ifanadiana, 950 m (Ward, P. S.); 40 km S Ambalavao,



Figs 19–22. Automontage images of workers of the *Tetraponera grandidieri* group, full-face (dorsal) view of head (19, 21) and lateral view of body (20, 22). 19, 20, *T. manangotra*, paratype (CASENT0121948); 21, 22, *T. variegata* (CASENT0409559).

Rés. Andringitra, 1275 m (Fisher, B. L.); 45 km S Ambalavao, 720 m (Fisher, B. L.); 7 km W Ranomafana Natl. Park, 1000 m (Steiner, K.); 7 km W Ranomafana Natl. Park, 1000 m (Steiner, W. E.; Zack, S.); 7 km W Ranomafana, 1000 m (Stebbins, M.; et al.); 7 km W Ranomafana, 900 m (Steiner, W. E.); 8 km E Kianjavato, 145 m (Alpert, G.); 9 km ESE Ranomafana, nr. Ifanadiana, 600 m (Ward, P. S.); FC Vatovavy, 175 m (Fisher, B. L.; et al.); Ivohibe, 1500 m (Decary, R.); Maharira Forest, Ranomafana Natl Pk, 1350 m (Rajeriarison, E.); Maharira Forest, Ranomafana Natl Pk, 1375 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 1050 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 700 m (Rajeriarison, E.); Pays de Betsileo, "Sud Central Madagascar" (Hildebrandt); P.N. Ranomafana, 0.4 km WSW park entrance, 900 m (Kavanaugh, D. H.; Kavanaugh, K. M.); P.N. Ranomafana, 1020 m (Harin'Hala, R.); P.N. Ranomafana, 1130 m (Harin'Hala, R.); P.N. Ranomafana, Vatoharanana, 4.1 km 231° SW Ranomafana, 1100 m (Fisher, B. L.; et al.); P.N. Ranomafana, Vohiparara, 1110 m (Harin'Hala, R.); PN Befotaka-Midongy, 940 m (Fisher, B. L.; et al.); R.S. Ivohibe, 8.0 km E Ivohibe, 1200 m (Fisher, B. L.); Ranomafana (Pauly, A.); Ranomafana N. P., 1000 m (Alpert, G.; et al.); Ranomafana N.P., Talatakely Forest, Piste S 100, 900 m (Rajeriarison, E.); Ranomafana N.P., Vohiparara Forest, 1200 m (Rajeriarison, E.); Ranomafana National Park, Talatakely, 915–1000 m (Lee, V. F.; Ribrado, K. J.); Ranomafana Natl Pk. (Rajeriarison, E.); Ranomafana Natl Pk., 950–1100 m (Bartolozzi, L.; et al.); Ranomafana Natl. Pk., Saharoemba ZP, 800 m (Rabeson, P.); Ranomafana NP, Talatakely (Griswold, C. E.; Ubick, D.); Ranomafana, Ambatolahy forest (Rajeriarison, E.); Ranomafana, Ambatovory forest, 1035 m (Rajeriarison, E.); Ranomafana, Miaranony Village (Kingman, A.); Ranomafana, Vohiparara forest, 1160 m (Rajeriarison, E.);

Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 10 km S Cap Este, 5 km W, 20 m (Alpert, G. D.); 14 km W Cap Est, Ambato, 100 m (Alpert, G. D.); 17 km W Andapa, Rés. d'Anjanaharibe-Sud, 875 m (Alpert, G. D.); 19 km ESE Maroantsetra, 250 m (Ward, P. S.); 19 km ESE Maroantsetra, 300 m (Ward, P. S.); 19 km ESE Maroantsetra, 350 m (Ward, P. S.); 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); 6.3 km S Ambanizana, Andranobe, 25 m (Fisher, B. L.); 6.5 km SSW Befingotra, Res. Anjanaharibe-Sud, 875 m (Fisher, B. L.); 6.9 km NE Ambanizana, 1080 m (Fisher, B. L.); 6.9 km NE Ambanizana, 650 m (Fisher, B. L.); 8 km ESE Andasibe (=Périnet), 800 m (Ward, P. S.); Ambodiriana, 125 m (Fisher, B. L.; et al.); Ampasimbe, 450 m (Betsch, J.-M.); Andasibe (Périnet) (Brooks, R. W.); Andasibe PN, 1025 m (Harin'Hala, R.); Anosibe An'ala [as "Nosibé, Village de l'Imerina"] (Sikora); Antongil (Mocquerys); Asanoreyo, 3 km W Anosibe An'ala (Raharimina, C.); Baie d'Antongil (c.u.); Betampona, 520 m (Fisher, B. L.; et al.); Kalalao, 100 m (Fisher, B. L.; et al.); Manakambahiny (Pauly, A.); Mont. Akirindro, 7.6 km 341° NNW Ambinanitelo, 600 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m (Fisher, B. L.; et al.); Nosey Mangabe (Alpert, G. D.); Nosy Mangabe, <5 m (Ward, P. S.); Nosy Mangabe, 150 m (Ward, P. S.); Nosy Mangabe, 20 m (Ward, P. S.); Nosy Mangabe, 300 m (Ward, P. S.); Nosy Mangabe, 3 m (Fisher, B. L.; et al.); P.N. Mantadia, 895 m (Ratsirarson, H. J.); Perinet (Noyes, J. S.; Day, M. C.); Perinet (Ross, E. S.); PN Mananara-Nord, 225 m (Fisher, B. L.; et al.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Besaky River, 760 m (Fisher, B. L.; et al.); PN Zahamena, Oribe River, 780 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); Saint Marie, Forêt de Kalalao (Madl); St. Marie (c.u.); Tampolo, 218 m (Fisher, B. L.; et al.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 420 m (Fisher, B. L.); 10 km NW Enakara, Rés. Andohahela, 430 m (Fisher, B. L.); 10 km SSW Eminiminy, 750 m (Rajeriarison, E.); 11 km NW Enakara, Rés. Andohahela, 800 m (Fisher, B. L.); 5 km NNW Isaka-Ivondro, Rés. Andohahela, 280 m (Ward, P. S.); 5 km WNW Mandiso, Rés. Andohahela, 400 m (Ward, P. S.); Col de Manangotry, c.30 km N Fort Dauphin, ~1000 m (Whitacre, D.); Forêt Ivohibe, 650 m (Fisher, B. L.; et al.); Fort Dauphin (Alluaud, C.); Manatantely, 100 m (Fisher, B. L.; et al.); P.N. Andohahela, 3.8 km 113° ESE Mahamavo, 900 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy,5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.); Rés. Andohahela, Marosohy, 600 m (Fisher, B. L.); Vallee d'Ambolo, Col de Sakalavana (Alluaud, C.); *province unknown*: "Central Madagascar" (Hildebrandt); "Centre de Madag" (Hildebrandt); "Madag." (Sikora); "Madagascar Centralis" (Hildebrandt); "Madagascar" (c.u.); "Madagascar" (de Gaulle, J.); "Madagascar" (Grandidier); "Madagascar" (Sikora); "Madagascar/(S.-E.)" (Decary, R.).

Worker measurements (n = 13). HW 1.01–1.44, HL 1.20–1.65, LHT 1.07–1.56, CI 0.77–0.88, FCI 0.15–0.17, REL 0.28–0.36, REL2 0.34–0.43, SI 0.74–0.81, FI 0.29–0.36, PLI 0.50–0.59, PWI 0.40–0.53.

Worker diagnosis. With characteristics of the *T. grandidieri* group (see above); basal margin of mandible edentate; anterior clypeal margin broadly convex and crenulate, directed forward, not anteroventrally; head relatively elongate (CI 0.77–0.88); metanotal spiracle more or less visible in lateral view of mesosoma, protruding dorsally in the mesopropodeal impression; dorsal face of propodeum broadly convex in lateral and posterior views; standing pilosity generally sparse; long paired setae (0.2–0.4 mm in length) distributed as follows: 1 pair between the frontal carinae, 1 pair on upper half of head, 1 pair on the pronotum, 0–2 pairs on the petiole; 1–2 pairs on the postpetiole; standing pilosity scattered on successive abdominal segments (gastric segments 1–4); short appressed to subdecumbent hairs absent or inconspicuous on most of body; integument mostly sublucid, with fine coriarious/puncticulate sculpture; body orange-brown, appendages lighter; head usually dark brown to brownish-black, but concolorous with rest of body in some northern populations (see discussion below); legs uniformly light orange-brown.

Comments. This species is typically bicolored with a black or dark brown head and the remainder of the body a contrasting orange-brown. This allows it to be distinguished from the other two species, *T. inermis* and *T. merita*, with which it is widely sympatric—both of these usually have the head more or less concolorous with the mesosoma. Some northern populations of *T. grandidieri* have workers that are unicolorous orange-brown, however, and these superficially resemble the other two species. They can be recognized because they lack a tooth on the basal margin of the mandible (present in *T. merita*) and the metanotal spiracle protrudes from the mesosoma dorsum in profile (not protruding in *T. inermis*). The degree of prominence of the metanotal spiracle varies, however, so it is also useful to examine head shape, which is more elongate in *T. grandidieri* (worker CI 0.77–0.88 versus 0.88–0.97 in *T. inermis*; see also additional discussion under *T. inermis*). *T. grandidieri* also overlaps in distribution with *T. hespera* in northern Madagascar. Where these two species co-occur *T. grandidieri* has a bicolored body, while *T. hespera* has a unicolored body and contrasting dark bands on the femora.

At Betampona (17°53′S 49°12′E) Brian Fisher collected three nest series of *T. grandidieri*: one (BLF13292) with unicolored workers, a second (BLF13298) with bicolored workers, and a third (BLF13349) with both unicolored and bicolored workers, in approximately equal proportions. The Betampona workers with light and dark heads show no obvious differences other than color. The occurrence of both forms in the same nest is consistent with the view that they are conspecific. In addition, genetic data (>10 kb of sequence data from several nuclear genes and one mitochondrial gene) from populations sampled throughout the range of the species show the two color forms to be phylogenetically comingled (Ward unpubl.).

Both color forms are here treated as conspecific but further studies are needed to clarify their status. It is possible that these color morphs show some degree of reproductive isolation and/or ecotypic differentiation. As indicated below, they appear to be involved in a mimicry complex with some species of *Camponotus*.

Finally it should be noted that there are nine specimens of *T. grandidieri* in the Forel collection in MHNG (Geneva) labeled as "Typus" or "Cotypus" but most are not true types, because the label data exclude this possibility. These non-types include three males (from Andrangoloaka), one dealate queen (from Andrangoloaka) and one worker (from "Nosibé, Village de l'Imerina"), all with a red "Typus" label, and an alate queen (Madagascar/Sikora) labeled "Cotypus". Only three workers in MHNG are apparently part of the actual type series of *T. grandidieri* (there is also a syntype worker in MCSN). To avoid confusion I have designated one of the MHNG syntype workers as lectotype.

Distribution and biology. *Tetraponera grandidieri* is widespread in eastern Madagascar, with a distribution that spans the length of the island (Fig. 23). Populations are restricted to rainforest, at elevations ranging from sea level to 1375 m. As a result of habitat destruction in the lowlands most populations are found at intermediate or higher elevations. Colonies usually occupy dead twigs or branches on the ground, less commonly in the lower canopy. During field work in Madagascar I collected thirteen nest series of this species, of which nine were in dead wood and four were located in cavities of live plants: three in stems of tree saplings (*Ixora* sp., *Leea* sp. and an unidentified plant), and one in a cavity in a live root of a tree in the genus *Rhus*. There were no scale insects (Coccoidea) in any of these live cavity nests, however, and there is no indication that *T. grandidieri* is closely associated with any particular plant species. It seems clear that it and other members of the *T. grandidieri*

group occupy moister nest sites than most *Tetraponera* species. The nests of *T. grandidieri* apparently contain no more than one dealate queen, and colony sizes are small (5–40 workers). Alate queens and males have been collected from February to May. Workers commonly forage on low vegetation, and they appear to be mimicked by members of the *Camponotus putatus* complex whose workers forage in similar microhabitats. *T. grandidieri* is generally absent from disturbed rainforest edge and other high light environments.

Tetraponera hespera sp. n.
(Figs 2–4, 6, 9–12, 24)

Tetraponera psw110; Fisher 2002: 318. Cited in faunal inventory.

Holotype worker. MADAGASCAR Antsiranana: Nosy Be, 4 km ESE Andoany (=Hellville), 100 m, 13°25'S 48°18'E, 2.v.1989, ex rotten stick on ground, rainforest, P. S. Ward#10457 (CASENT0012865) (CASC).

Paratypes. Series of workers and queens, same locality and date as holotype, elevation 100–200 m (P. S. Ward#10456, 10457, 10459, 10463, 10465, 10470-1) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, MCZC, PSWC, SAMC, UCDC) MADAGASCAR *Antsiranana*: Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Fisher, B. L.; et al.); Forêt Antsahabe, 11.4 km 275° W Dairana, 550 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.); Nosy Be, 4 km ESE Andoany (=Hellville), 100 m (Ward, P. S.); Rés. Ankarana, 7 km SE Matsaborimanga, 150 m (Ward, P. S.); Rés. Spéc. Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m (Alpert, G. D.; et al.); Rés. Spéc. Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m (Fisher, B. L.; et al.); Rés. Spéc. Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m (Fisher, B. L.; et al.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m (Fisher, B. L.); *Toliara*: Ambohijanahary, 34.6 km 314° NW Ambaravaranala, 1100 m (Fisher, B. L.; et al.); Ambohijanahary, 35.2 km 312° NW Ambaravaranala, 1050 m (Fisher, B. L.; et al.).

Worker measurements (n = 13). HW 0.95–1.31, HL 1.19–1.55, LHT 1.12–1.53, CI 0.78–0.90, FCI 0.14–0.18, REL 0.30–0.35, REL2 0.35–0.41, SI 0.77–0.83, FI 0.29–0.34, PLI 0.50–0.58, PWI 0.42–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; head relatively elongate (CI 0.78–0.90); metanotal spiracle visible in lateral view of mesosoma (Fig. 6); dorsal face of propodeum usually broadly convex in posterior view, but more dorsally compressed and subtriangular in one population (see below); standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarious/puncticulate sculpture; body unicolorous yellow-brown or orange-brown, legs usually with contrasting black bands on the distal portions of the femora; banding sometimes weakly developed on the profemur, and absent from all legs in one population.

Comments. *T. hespera* represents an assemblage of variably isolated populations in northwestern Madagascar. This species is most readily recognized by its distinctive color pattern: workers are usually a unicolorous yellow-brown or orange-brown, with contrasting black bands on the legs (Fig. 10). In earlier identifications of museum material I employed a code name for this species: *Tetraponera* psw110.

The *hespera*-like population occupying the Ankarana Massif is divergent in several respects: workers lack the characteristic black leg banding (Fig. 12) and they have a dorsally narrowed propodeum that appears more or less triangular in shape when seen in posterior view (Fig. 3), in contrast to the broadly convex propodeum seen in other populations of *T. hespera* (Fig. 4) and in the rest of the *T. grandidieri* group. Although I considered treating the

Ankarana form as a different species, several observations argued against this. (1) It is strictly allopatric to the more typical morph of *T. hespera*, so there is no "test" of species distinctness in sympatry. (2) Samples from tropical dry forest at Forêt Antsahabe, 60 km southeast of Ankarana, have black leg banding but the propodeum tends to be intermediate in shape between the Ankarana morph and more typical *T. hespera*. (3) A worker (BLF10881; CASENT0053718) from another nearby locality, Forêt Binara, has black leg banding and a broadly convex propodeal dorsum—yet it is genetically identical at the mitochondrial COI locus to a worker from Forêt Antsahabe. The COI data indicate that all three populations (Ankarana, Antsahabe and Binara) are closely related and form a clade that is sister to *T. hespera* + *T. hirsuta*, but with combined nuclear gene sequences the three populations do not form a clade; instead, they are paraphyletic with respect to *T. hirsuta*. Thus, recognizing the Ankarana form as a distinct species would require an arbitrary division along a gradient of differentiated allopatric populations.

Distribution and biology. This species is found in northwestern Madagascar, with an isolated population at Ambohijanahary in central western Madagascar (Fig. 24). It occurs sympatrically with *T. grandidieri*, *T. hirsuta* and *T. merita* at one or more localities. Most populations of *T. hespera* are in seasonally dry rainforest, where colonies tend to nest near the ground level, usually in rotten sticks. One colony from the type locality (PSW10456) was nesting in an earthworm cast on the ground. As in *T. grandidieri*, observed colony sizes are small (4–36 workers).

Tetraponera hirsuta sp. n.

(Figs 13–14, 25)

Holotype worker. MADAGASCAR Antsiranana: R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m, 13°57.7′S 48°26.0′E, 8.xi.1998, ex sifted litter, rainforest, B. L. Fisher#1996 (CASENT0170370) (CASC).

Paratypes. 1 worker, 1 dealate queen, same locality and date as holotype, ex rotting tree stump, rainforest (B. L. Fisher#2008; CASENT0170371); 1 worker, MADAGASCAR Antsiranana: R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m, 11.xi.1998, ex sifted litter, rainforest (B. L. Fisher#1862; CASENT0170368) (CASC); 2 workers, MADAGASCAR Antsiranana: R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m, 12.xi.1998, beating low vegetation, rainforest (B. L. Fisher#1888; CASENT0170369) (CASC).

Material Examined.—Known only from the type material.

Worker measurements (n = 2). HW 1.19–1.34, HL 1.35–1.51, LHT 1.32–1.45, CI 0.88–0.89, FCI 0.15, REL 0.34, REL2 0.39, SI 0.73–0.76, FI 0.33–0.34, PLI 0.57, PWI 0.51–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; scape with conspicuous suberect and subdecumbent hairs (Fig. 13); standing pilosity and appressed pubescence generally sparse elsewhere, although tending to be better developed than in other species in the *grandidieri* group; integument mostly sublucid, with fine coriarious/puncticulate sculpture; body tricolored: metasoma, appendages, and ventral margin of mesosoma orange, most of mesosoma reddish-brown, and head dark brownish black.

Comments. *T. hirsuta* can be distinguished from related species by the more conspicuous pilosity on the scapes (Fig. 13) and the tricolored body. The differences are slight but consistent, and they are maintained in sympatry with the otherwise similar species *T. grandidieri* and *T. hespera*.

Distribution and biology. This species appears to be endemic to the Manongarivo

Massif (Fig. 25), where it occurs sympatrically with *T. grandidieri*, *T. hespera* and *T. merita*. The only nest series is incomplete: one worker and one dealate queen from a rotting tree stump (BLF2008). Habits are assumed to be similar those of other species in the *T. grandidieri* group, but almost nothing is known about the biology of *T. hirsuta*.

Tetraponera inermis sp. n.
(Figs 5, 15–16, 25)

Tetraponera psw81; Fisher 1996: 100; Fisher 1999: 134. Cited in faunal inventories.

Holotype worker. MADAGASCAR Toamasina: 1 km SSW Andasibe (=Périnet), 920 m, 18°56′S 48°25′E, 16.xi.1990, ex rotten stick on ground, rainforest, P. S. Ward#10941 (CASENT0012862) (CASC).

Paratypes. Series of workers and queens, same locality as holotype, 16.xi.1990 and 12.xii.1990 (P. S. Ward#10940, 19041, 11143) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, CUIC, MCZC, NHMV, PSWC, SAMC, UCDC) MADAGASCAR *Fianarantsoa*: 43 km S Ambalavao, Res. Andringitra, 825 m (Fisher, B. L.); 8 km E Kianjavato, 145 m (Alpert, G.); FC Vatovavy, 175 m (Fisher, B. L.; et al.); Manombo, 30 m (Fisher, B. L.; et al.); R.S. Ivohibe, 7.5 km ENE Ivohibe, 900 m (Fisher, B. L.); Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); Andasibe (Périnet) (Brooks, R. W.); F.C. Andriantantely, 530 m (Ratsirarson, H. J.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Perinet (Noyes, J. S.; Day, M. C.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); Res. Perinet-Analamazotra, 930–1040 m (Olson, D. M.); Res. Perinet-Analamazotra, 950 m (Olson, D. M.); vic. Andasibé (=Perinet), 950–980 m (Brown, W. L.; Brown, D. E.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 430 m (Fisher, B. L.); 10 km SSW Eminiminy, 750 m (Rajeriarison, E.); 11 km NW Enakara, Rés. Andohahela, 800 m (Fisher, B. L.); 5 km NNW Isaka-Ivondro, Rés. Andohahela, 280 m (Ward, P. S.); 5 km WNW Mandiso, Res. Andohahela, 400 m (Rajeriarison, E.); 5 km WNW Mandiso, Rés. Andohahela, 400 m (Ward, P. S.); 6 km SSW Eminiminy, 250 m (Alpert, G. D.); 6 km SSW Eminiminy, 250 m (Rabeson, P.); 6 km SSW Eminiminy, 250 m (Rajeriarison, E.); 6 km SSW Eminiminy, Rés. Andohahela, 330 m (Ward, P. S.); 9 km SSW Eminiminy, Rés. Andohahela, 500 m (Ward, P. S.); Forêt Ivohibe, 200 m (Fisher, B. L.; et al.); Fort Dauphin (c.u.); Grand Lavasoa, 450 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy, 5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.).

Worker measurements (n = 11). HW 1.02–1.27, HL 1.05–1.42, LHT 1.05–1.38, CI 0.88–0.97, FCI 0.12–0.15, REL 0.31–0.36, REL2 0.35–0.39, SI 0.72–0.76, FI 0.29–0.31, PLI 0.50–0.55, PWI 0.43–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; head relatively broad (CI 0.88–0.97); metanotal spiracle not visible in lateral view of mesosoma (Fig. 5), subtended laterally and anterolaterally by a pair of concavities that are separated by a transverse carina; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarious/puncticulate sculpture; head and mesosoma reddish-brown, upper part of propodeum often a darker red than rest of mesosoma; metasoma and appendages paler.

Comments. The worker of this species can be recognized by the absence of a tooth on the basal margin of the mandible; the more or less concolorous reddish-brown body (the upper half of propodeum is often a richer dark red, and the metasoma is paler); and the lack of a protruding metanotal spiracle when the mesosoma is viewed in profile (Fig. 5). In addition, the head tends to be broader than that of *T. grandidieri* and *T. hespera* (CI 0.88–0.97, versus 0.77–0.88 in *T. grandidieri* and 0.78–

0.90 in *T. hespera*). From *T. hespera* it can also be distinguished by the ratio of metatibial length to head width (LHT/HW 1.02–1.09 in *T. inermis*, and 1.10–1.22 in *T. hespera*).

In earlier identifications of museum material I assigned the code name *Tetraponera* psw81 to this species. During initial examination of *Tetraponera hirsuta* I misidentified it as *T. inermis*, using the code name *Tetraponera* psw81. This is the basis for the record of "*Tetraponera* psw081" from Manongarivo (Fisher 2002: 318). In fact, *T. inermis* is not known from that region.

In the Forel collection (MHNG, Geneva) there is a problematic worker from "Nosibé, village de l'Imerina" [=Anosibe an'Ala at 19°26'S 48°13'E] (leg. Sikora). This worker is large (HW 1.49, LHT 1.79) and unicolored, with an elongate head (CI 0.78), yet the metanotal spiracles are not protruding in lateral view. This individual combines features of *T. inermis* and *T. grandidieri* (unicolored form). At the moment I am unable to identify it with certainty.

Distribution and biology. *T. inermis* occurs in eastern Madagascar from Montagne d'Anjanaharibe to the vicinity of Tolagnaro (Fort Dauphin) (Fig. 25). Collections all come from rainforest, at elevations ranging from 30 m to 1040 m. Nests are located in rotten sticks on the ground, and are small in size. At the type locality I found one dealate queen gleaning the surfaces of leaves, walking rapidly and raising her gaster in the air. She then returned to her nest—a cavity in a small soft dead twig on the ground—which proved to contain eggs, larvae and worker pupae. Thus, this species exhibits non-claustral colony-founding, a trait presumably shared with other members of the *T. grandidieri* group. The gaster-raising behavior was observed in foraging workers of *T. inermis* but not those of the other two species with which *T. inermis* is sympatric: *T. grandidieri* and *T. merita*. *Camponotus reaumuri* Forel (related to *C. putatus* Forel) is a possible mimic of *T. inermis*.

Tetraponera manangotra sp. n.
(Figs 19–20, 24)

Holotype worker. MADAGASCAR Toliara: PN Andohahela, Manangotry, 33.8 km NW Tolagnaro, 575 m, 24°45.07'S 46°51.47'E, 24.xi.2006, ex dead twig above ground, rainforest, B. L. Fisher#15267 (CASENT0120025) (CASC).

Paratypes. Series of workers and dealate queens, same data as holotype (BMNH, CASC, MCZC, PSWC, SAMC, UCDC); 1 worker, MADAGASCAR Toliara: PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 275 m, 24°45.52'S 46°51.22'E, 23.xi.2006, beating low vegetation, rainforest, B. L. Fisher#15166 (CASENT0121948) (CASC).

Material Examined.—Known only from the type material.

Worker measurements (n = 4). HW 1.48–1.58, HL 1.77–2.01, LHT 1.64–1.76, CI 0.79–0.83, FCI 0.14–0.16, REL 0.28–0.31, REL2 0.36–0.37, SI 0.77–0.78, FI 0.32–0.33, PLI 0.49–0.55, PWI 0.61–0.65.

Worker diagnosis. Matching the diagnosis of the *T. grandidieri* group (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin convex, directed forward, and protruding medially; posterior margin of head with low, sharp transverse crest, about 0.30 mm long; metanotal spiracle visible in lateral view of mesosoma; mesopropodeal impression sharply incised; dorsal face of propodeum somewhat flattened, propodeum subquadrate in posterior view; petiole broad and robust, appearing subtriangular in lateral and dorsal views; maximum petiole width about half of head width (DPW/HW 0.50–0.53); anterior peduncle of petiole short and broad; standing pilosity and appressed pubescence similar to that of *T. grandidieri* but with greater number of standing hairs (4–8) on petiole and postpetiole; integument mostly sublucid, with fine coriarious/puncticulate sculpture, coarser transverse rugulae on side of mesosoma; body reddish-brown, appendages (except mesofemur and meta-

femur) paler; distal half of flagellum infuscated.

Comments. *T. manangotra* departs somewhat from the general habitus of the *T. grandidieri* group. The protruding median clypeal lobe, strong crest on the posterior margin of the head, and robust petiole are quite distinctive. In dorsal view the petiole is subtriangular in shape and its maximum width is half the head width. In other species in the *T. grandidieri* group the petiole is more slender, not exceeding two-fifths of the head width (DPW/HW 0.30–0.40) and the posterolateral corners of the petiole are broadly rounded. Large size (HW > 1.46, LHT > 1.62) alone separates *T. manangotra* from all other species in the *T. grandidieri* group except *T. merita*. From the latter it can be distinguished by the features mentioned above, as well as the absence of a tooth on the basal margin of the mandible and the more elongate head (CI 0.79–0.83 in *T. manangotra* versus 0.90–0.94 in *T. merita*).

Distribution and biology. This species is known from a single nest series from Col de Manangotry and a foraging worker collected at an adjacent site (Col de Tanatana), in Parc National Andohahela, in rainforest of extreme southern Madagascar. The nest was in a dead twig above the ground, and comprised 5 dealate queens, 47 workers, larvae, prepupae, worker pupae, male pupae and queen pupae. Although the dealate queens were not dissected to evaluate their reproductive state, it seems likely that this species is functionally polygynous. The queens (HW 1.50–1.56, n = 5) are about the same size as the workers, whereas in other species in the *T. grandidieri* group (and in most other *Tetraponera*) the queens are notably larger than the workers.

Tetraponera merita sp. n.
(Figs 1, 17–18, 26)

Sima Grandidieri var. *Hildebrandti*; Forel 1892: 260 (in part) (misidentification)

Tetraponera psw92; Fisher 1996: 100; Fisher 1998: 49; Fisher 1999: 134; Fisher 2002: 318. Cited in faunal inventories.

Holotype worker. MADAGASCAR Toamasina: 1 km SSW Andasibe (=Périnet), 920 m, 18°56'S 48°25'E, 16.xi.1990, ex rotting tree stump, rainforest, P. S. Ward#10943 (CASENT0012863) (CASC).

Paratypes. Series of workers and queens, same locality as holotype, 16.xi.1990 and 12.xii.1990 (P. S. Ward#10939, 19043, 10944-3, 11144) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, MCZC, MHNG, MNHN, NHMV, PSWC, SAMC, UCDC) MADAGASCAR *Antsiranana*: Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Fisher, B. L.; et al.); Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Rafanomezantsoa, J. J.); Forêt Antsahabe, 11.4 km 275° W Dairana, 550 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.; et al.); P.N. Marojejy, 27.6 km 35° NE Andapa, 775 m (Fisher, B. L.; et al.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m (Fisher, B. L.); *Fianarantsoa*: 43 km S Ambalavao, Res. Andringitra, 800 m (Fisher, B. L.); 43 km S Ambalavao, Res. Andringitra, 825 m (Fisher, B. L.); 45 km S Ambalavao, 785 m (Fisher, B. L.); Ambodiamontana [as "Ambodiamatana"], Ranomafana Natl Pk, 800 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 1050 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 700 m (Rajeriarison, E.); Nat. Park Ranomafana, Miaranony, 1050 m (Rajeriarison, E.); P.N. Ranomafana, 1130 m (Harin'Hala, R.); P.N. Ranomafana, Vatoharanana, 4.1 km 231° SW Ranomafana, 1100 m (Fisher, B. L.; et al.); PN Befotaka-Midongy, 940 m (Fisher, B. L.; et al.); R.S. Ivohibe, 8.0 km E Ivohibe, 1200 m (Fisher, B. L.); R.S. Ivohibe, 9.0 km NE Ivohibe, 900 m (Fisher, B. L.); Ranomafana Natl Pk. (Rajeriarison, E.); Ranomafana, Miaranony Village (Kingman, A.); Valoloaka Forest, Ranomafana Natl Pk, 1150 m (Rajeriarison, E.); Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 17 km W Andapa, Res. d'Anjanaharibe-Sud, 875 m (Alpert, G. D.); 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); 6.5 km SSW Befingotra, Res. Anjanaharibe-

Sud, 875 m (Fisher, B. L.); 9.2 km WSW Befingotra, Res. Anjanaharibe-Sud, 1280 m (Fisher, B. L.); Andasibe (Périnet) (Brooks, R. W.); Betampona, 390 m (Fisher, B. L.; et al.); Betampona, 520 m (Fisher, B. L.; et al.); F.C. Andriantantely, 530 m (Ratsirarson, H. J.); F.C. Sandranantitra, 450 m (Ratsirarson, H. J.); Forêt Ambatovy, 14.3 km 57° [NE] Moramanga, 1075 m (Fisher, B. L.; et al.); Forêt Analamay, 19.1 km 51° NE Moramanga, 1068 m (Fisher, B. L.; et al.); Forêt Torotorofotsy, 14.9 km 71° ENE Moramanga, 1070 m (Fisher, B. L.; et al.); Manakambahiny (Pauly, A.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m (Fisher, B. L.; et al.); P.N. Mantadia, 895 m (Ratsirarson, H. J.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Besaky River, 760 m (Fisher, B. L.; et al.); PN Zahamena, Oribe River, 780 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); vic. Andasibé (=Perinet), 950–980 m (Brown, W. L.; Brown, D. E.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 420 m (Fisher, B. L.); Env. de Tsivory (Région du Sud) (Vacher); Forêt Ivohibe, 200 m (Fisher, B. L.; et al.); Forêt Ivohibe, 650 m (Fisher, B. L.; et al.); Fort Dauphin (Sikora); Grand Lavasoa, 450 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy, 5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.); *province unknown*: "Madagascar Central" (Sikora); "Madagascar/(S.-E.)" (Decary, R.).

Worker measurements (n = 9). HW 1.16–1.59, HL 1.23–1.74, LHT 1.38–1.83, CI 0.90–0.94, FCI 0.11–0.15, REL 0.31–0.34, REL2 0.34–0.38, SI 0.76–0.82, FI 0.28–0.32, PLI 0.49–0.56, PWI 0.46–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible with conspicuous tooth (Fig. 1); anterior clypeal margin deflected ventrally; head relatively broad (CI 0.90–0.94); metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarious/puncticulate sculpture; orange to reddish-brown, appendages paler; head usually concolorous with mesosoma.

Comments. This is one of the more distinctive species in the *T. grandidieri* group, easily recognized by the presence of a tooth on the basal margin of the mandible and by the undercut median portion of the clypeus. *T. merita* is usually more or less unicolorous reddish- or orange-brown, without a contrastingly darker head, but in some northern populations (3.9 km S Ambaliha, Forêt Antsahabe and Forêt Binara) the head is infuscated relative to the rest of the body. This species also tends to be larger than all the others except *T. manangotra* (see HW, HL and LHT measurements). Although the holotype of *T. grandidieri hildebrandti* (Forel, 1891) is conspecific with *T. grandidieri* (Forel, 1891), material referred to *T. g. hildebrandti* by Forel (1892: 260) includes *T. merita*. During earlier examination and identification of museum material I assigned the code name *Tetraponera* psw92 to this species.

Distribution and biology. *T. merita* is widely distributed in rainforest of eastern and northern Madagascar, overlapping the ranges of all other species in the *T. grandidieri* group (Fig. 26). Nests have been found on the ground in rotten logs, sticks and tree stumps. A worker from the type series (PSW10943) stung me on my left index finger. The sting was rather painful and left a pustule that lasted more than a week. It reinforced my impression that the conspicuous orange and reddish-brown coloration of workers of *T. merita* and related species in the *T. grandidieri* group is aposematic.

Tetraponera variegata (Forel 1895) stat. n.
(Figs 21–22, 24)

Sima Grandidieri var. *variegata* Forel 1895: 487. Syntypes, 2 workers, "Centr Madag." (Sikora) (MHNG) [examined] [Imaged on AntWeb: CASENT0101045, CASENT0101046]. **Syn. n.** One syntype (CASENT0101046) here designated **lectotype**.

Tetraponera grandidieri var. *variegata* (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

Tetraponera grandidieri var. *variegata* (Forel); Santschi 1926: 27. Description of queen.

Material Examined.—(CASC, MHNG, NHMB, PSWC) MADAGASCAR *Antananarivo*: 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m (Fisher, B. L.; et al.); *Antsiranana*: PN Marojejy, 488 m (Irwin, M. E.); *Fianarantsoa*: 7 km W Ranomafana, 1100 m (Steiner, W. E.); Ranomafana National Park, Talatakely, 850 m (Irwin, M. E.; Schlinger, E. I.); RS Kalambatritra, Ampanihy, 1269 m (Fisher, B. L.; et al.); *Toamasina*: Moramanga (Descarpentries); Morarano-Chrome (Pauly, A.); *Toliara*: Forêt Ivohibe, 650 m ((Fisher, B. L.; et al.); *province unknown*: "Centr Madag." (Sikora).

Worker measurements (n = 6). HW 1.15–1.36, HL 1.36–1.62, LHT 1.39–1.59, CI 0.80–0.85, FCI 0.13–0.17, REL 0.29–0.32, REL2 0.35–0.38, SI 0.76–0.81, FI 0.30–0.32, PLI 0.49–0.55, PWI 0.41–0.46.

Worker diagnosis. Similar to *T. grandidieri* (q.v.), but larger on average. Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarious/puncticulate sculpture; mesosoma, petiole and postpetiole orange-brown, head and gaster a contrasting blackish brown, legs with a black band on the distal portions of the femora.

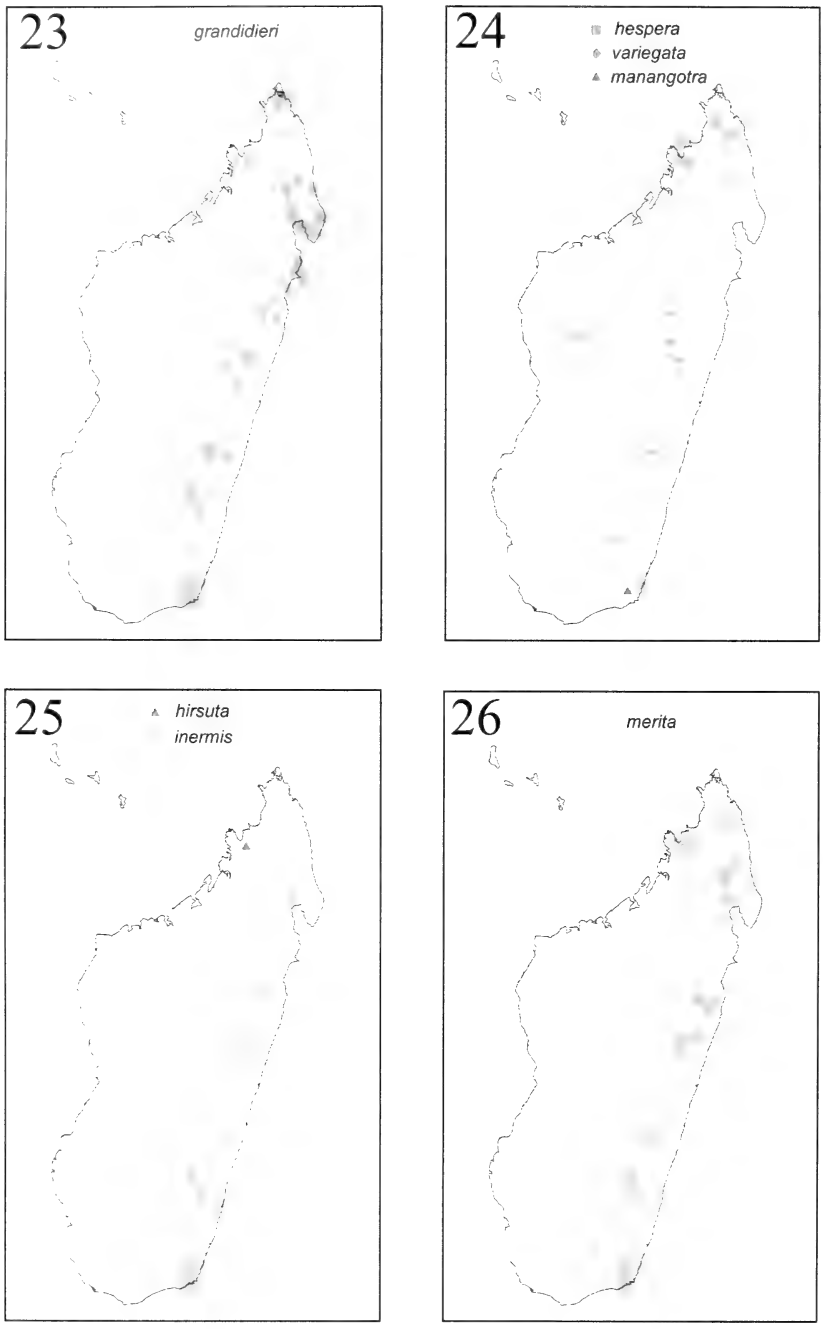
Comments. *T. variegata* can be distinguished from related species by the bicolored body and black banded legs (Fig. 22). *T. grandidieri* lacks black banding on the legs and, although the body is often bicolored, only the head is dark, not the head and gaster (as in *T. variegata*). Although such color differences might appear to be a weak basis for treating *T. variegata* as a species distinct from *T. grandidieri*, the two forms have been collected sympatrically at several sites (PN Marojejy, PN Ranomafana, Forêt Ivohibe) without showing any signs of intergradation. One other species, *T. hespera*, from northwestern Madagascar, exhibits black leg banding in most populations but in that species the body is unicolored light yellow or orange-brown.

I have designated a lectotype for *T. variegata* since there is a dealate queen in NHMB (Basel) from Moramanga (leg. Descarpentries) labeled, incorrectly, as a *variegata* "type". This specimen has no status as a type, but it reflects the practice of earlier myrmecologists of designating "type specimens" for queens and males when they were described later than the worker caste of the same species.

Distribution and biology. *T. variegata* is known from several widely scattered locations in the rainforest zone of eastern Madagascar (Fig. 24). Its range broadly overlaps the distributions of *T. grandidieri*, *T. inermis* and *T. merita*. Specimens have been collected in Malaise traps and foraging on vegetation. Up to this point no nests have been found.

CONCLUDING REMARKS

Workers of closely related ant species can often be distinguished by differences in pilosity, sculpture and shape. Yet the species in the *Tetraponera grandidieri* group show quite limited divergence with respect to these kinds of characters. A brief examination of the male genitalia of four species (*T. grandidieri*, *T. hespera*, *T. inermis* and *T. merita*) failed to yield any obvious differences in the shapes of the aedeagus, paramere or subgenital plate (abdominal sternite 9), even though male genitalia often provide useful differences among closely related species in other groups of pseudomyrmecine ants (Ward 1999, 2001). Nevertheless the species recognized here occur sympatrically in various combinations and the slight differences between them are not blurred where they co-occur. I



Figs 23–26. Distribution of the *Tetraponera grandidieri* group. 23, *T. grandidieri*; 24, *T. hespera* (squares), *T. variegata* (diamonds) and *T. manangotra* (triangle); 25, *T. hirsuta* (triangle) and *T. inermis* (squares); 26, *T. merita*.

conclude that although the taxa are likely to have diverged relatively recently they behave as good biological species. The ants have painful stings and their bright orange-brown or reddish-brown colors appear to have an aposematic function—as is also indicated by the occurrence of non-stinging *Camponotus* ants whose work-

ers mimic those of the *T. grandidieri* group. It would be interesting to investigate the role of warning coloration and mimicry in maintaining species distinctness in this group.

ACKNOWLEDGMENTS

The following individuals provided access to material in the indicated collections: Barry Bolton (BMNH), Brian Fisher and Wojciech Pulawski (CASC), Roberto Keller (CUIC), Roberto Poggi and Valter Raineri (MCSN), Gary Alpert and Stefan Cover (MCZC), Claude Besuchet, Ivan Löbl, and Bernard Merz (MHNG), Janine Casevitz-Weulersse (MNHN), Michel Brancucci (NHMB), Max Fischer and Stefan Schödl (NHMV), Hamish Robertson (SAMC) and Ted Schultz (USNM). I also received several samples of the *Tetraponera grandidieri* group from Dave Olson and Dave Whitacre. I am especially grateful to Brian Fisher (CAS) whose collections from Madagascar have increased the geographic coverage and comprehensiveness of sampling of the ant fauna to an unprecedented degree, and whose development of AntWeb (www.antweb.org) has greatly facilitated the study of ants, in Madagascar and elsewhere. Automontage images of the *Tetraponera* species were taken by April Nobile and Erin Prado at CAS. During several field trips to Madagascar in the period 1989–1993 I was given helpful advice and logistical support by Gary Alpert, Steve Goodman, Claire Kremen, Vincent Razafimahatratra, and George Schatz. Brian Fisher provided useful comments on an earlier version of the manuscript. This research was supported by a series of NSF grants, most recently DEB-0344731 and EF-0431330.

LITERATURE CITED

Brady, S. G., B. L. Fisher, T. R. Schultz, and P. S. Ward. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences U. S. A.* 103: 18172–18177.

Coyne, J. A. and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Sunderland, MA, xiii + 545 pp.

Fisher, B. L. 1996. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana Zoology* (n.s.) 85: 93–108.

———. 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. *Fieldiana Zoology* (n.s.) 90: 39–67.

———. 1999. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andohahela, Madagascar. *Fieldiana Zoology* (n.s.) 94: 129–147.

———. 2002. Ant diversity patterns along an elevational gradient in the Réserve Spéciale de Manongarivo, Madagascar. *Boissiera* 59: 311–328.

———. 2003. Formicidae, ants. *in* Goodman, S. M., and J. P. Benstead eds. *The natural history of Madagascar*. University of Chicago Press, Chicago, pp. 811–819.

Forel, A. 1891. Les Formicides [part]. In: Grandidier, A. *Histoire physique, naturelle, et politique de Madagascar. Volume XX. Histoire naturelle des Hyménoptères. Deuxième partie (28e fascicule)*. Hachette et Cie, Paris, v + 237 pp.

———. 1892. Les Formicides [concl.]. In: Grandidier, A. *Histoire physique, naturelle, et politique de Madagascar. Volume XX. Histoire naturelle des Hyménoptères. Deuxième partie. Supplèment au 28e fascicule*. Hachette et Cie, Paris, pp. 229–280.

———. 1895. Quelques fourmis du centre de Madagascar. *Annales de la Société Entomologique de Belgique* 39: 485–488.

Huber, B. A. 2003. Cladistic analysis of Malagasy pholcid spiders reveals generic level endemism: Revision of *Zatavua* n. gen. and *Paramicromerys* Millot (Pholcidae, Araneae). *Zoological Journal of the Linnean Society* 137: 261–318.

Lees, D. C., C. Kremen, and L. Andriamampianina. 1999. A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biological Journal of the Linnean Society* 67: 529–584.

Mayr, E. 1963. *Animal species and evolution*. Belknap Press of Harvard University Press, Cambridge, MA, xiv + 797 pp.

Santschi, F. 1926. Trois notes myrmécologiques. *Annales de la Société Entomologique de France* 95: 13–28.

United States Board on Geographic Names. 1989. *Gazetteer of Madagascar. Second Edition*. Defense Mapping Agency, Washington, DC, xvii + 826 pp.

Viette, P. 1991. Faune de Madagascar, supplément 2. Principales localités où des insects ont été recueillis à Madagascar. Chief field stations where insects were collected in Madagascar. Published by the author (Imprimerie Némont, Bar-sur-Aube, France), 88 pp.

Ward, P. S. 1991. Phylogenetic analysis of pseudomyrmecine ants associated with domatia-bearing plants., *in* Huxley, C. R., and D. F. Cutler eds. *Ant-plant interactions*. Oxford University Press, Oxford, pp. 335–352.

———. 1999. Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae), *Triplaris*- and *Tachigali*-inhabiting ants. *Zoological Journal of the Linnean Society* 126: 451–540.

———. 2001. Taxonomy, phylogeny and biogeography of the ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian regions. *Invertebrate Taxonomy* 15: 589–665.

———. 2006. The ant genus *Tetraponera* in the Afrotropical region: synopsis of species groups and revision of the *T. ambigua*-group (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 8: 119–130.

——— and D. A. Downie. 2005. The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): phylogeny and evolution of big-eyed arboreal ants. *Systematic Entomology* 30: 310–335.

Wheeler, W. M. 1922. Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. *Bulletin of the American Museum of Natural History* 45: 1005–1055.

J. HYM. RES.
Vol. 18(2), 2009, pp. 305–314

A New North American Species of *Pogonomyrmex* (Hymenoptera: Formicidae) from the Mohave Desert of Eastern California and Western Nevada

ROBERT A. JOHNSON AND RICK P. OVERSON

School of Life Sciences, Arizona State University, Tempe, AZ, 85287-4501, USA

Abstract.—***Pogonomyrmex mohavensis* Johnson sp. nov.** is described from the Mohave Desert of eastern California and western Nevada, USA. A mitochondrial phylogeny affirmed taxonomic validity of *P. mohavensis*, and inferred that it is most closely related to *Pogonomyrmex snellingi*. Field observations and a distribution map for *P. mohavensis* are also provided, along with an updated key to *Pogonomyrmex californicus* group species that occur in central and western North America. *Pogonomyrmex mohavensis* can be separated from other *P. californicus* group species based on a unique combination of characters that include: (1) six mandibular teeth (very rarely with a small seventh denticle), and (2) in side view, the cephalic rugae extend more or less directly to the vertex and do not converge posterior to the eyes or form circumocular whorls. All other *P. californicus* group species have 7–8 mandibular teeth (six in *Pogonomyrmex anzensis*) and the cephalic rugae almost always converge posterior to the eyes or form circumocular whorls.

Key words.—*Pogonomyrmex*, new species, Mohave Desert, *P. californicus* species group, mitochondrial phylogeny

The seed-harvester ant genus *Pogonomyrmex* Mayr, 1868 is an exclusively New World group that consists of approximately 64 described species (Bolton et al. 2006; Lattke 2006) that occur throughout much of North and South America. In the American West, Mexico, and southern South America, these are ecologically dominant ants, especially in arid habitats. The modern study of the genus began with Cole's (1968) stellar revision of North American species. This monograph stabilized the taxonomy of this group and set the stage for studies of ecology, biogeography, territoriality, mating behavior, communication, caste determination, and foraging behavior that have greatly facilitated our understanding of ant biology (Anderson et al. 2006; Gadau et al. 2003; Hölldobler 1976a, 1976b; Johnson 2000, 2001; Taber 1998). Since the publication of Cole's study, several additional new species have been described from North America and perhaps several more remain to be discovered, especially in Mexico (e.g., Vásquez-Bolaños and MacKay 2004). This paper describes a new species of *Pogonomyrmex* from the Mohave Desert of eastern California and western Nevada, USA.

MATERIALS AND METHODS

Measurements and Indices

Morphological characters were photographed using a Spot Insight QE camera attached to a Leica MZ 125 microscope. Images were then projected onto a video monitor, and characters were measured using ImageJ (available at http://rsb.info.nih.gov/nih-image/). Measurements were calibrated using photographs of an ocular micrometer scaled in 0.01 mm increments. The following standard measurements are used:

HL **Head Length**: length of the head capsule excluding mandibles, in full-face view, from the midpoint of the anterior cly-

peal margin to the midpoint of the occipital margin.

HW **Head Width**: maximum width of the head immediately behind the eyes, measured in full-face view.

CI **Cephalic Index**: (HW/HL) × 100.

MOD **Maximum Ocular Diameter**: maximum diameter of the eye measured with the head in full lateral aspect.

OI **Ocular Index**: (MOD/HW) × 100.

OMD **Oculo-Mandibular Distance**: minimum distance from the anterior eye margin to the nearest point of the malar area (base of mandible).

SL **Scape Length**: maximum straight line length of the antennal scape from apex to base.

SI **Scape Index**: (SL/HW) × 100.

PNW **Pronotal Width**: maximum width of the pronotum, as seen from above, measured at a right angle to the longitudinal axis of the mesosoma.

HFL **Hind Femur Length**: measured along the dorsal margin from the articulation with the trochanter to most distal tip of the femur.

HFI **Hind Femur Index**: (HFL/HW) × 100.

ML **Mesosoma Length**: diagonal length of the alitrunk in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobe.

PW **Petiole Width**: maximum width of petiole, as seen from above, at a right angle to the longitudinal axis of the mesosoma.

PPW **Postpetiole Width**: maximum width of postpetiole, as seen from above, at a right angle to the longitudinal axis of the mesosoma.

Abbreviations of Depositories

CASC	California Academy of Sciences, San Francisco, California, USA
CIDA	Orma J. Smith Museum of Natural History, The College of Idaho, Caldwell, Idaho, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
RAJC	Robert A. Johnson collection, Tempe, Arizona, USA
UCDC	Bohart Museum of Entomology, University of California, Davis, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
WPMC	William P. MacKay collection, El Paso, Texas, USA

Molecular Analyses and Phylogenetic Inferences

We constructed a phylogeny using a 653 base-pair sequence of the cytochrome oxidase I mitochondrial gene to affirm taxonomic status of *P. mohavensis* and to infer its relationship with other species in the *P. californicus* group. The phylogeny included multiple samples from sympatric colonies of *P. mohavensis* and *P. californicus*, with the latter species being the only other *P. californicus* group species that occurred at or near the type locality; samples of the four other species in the *P. californicus* group were also included (Table 1). We also included samples of *P. anzensis*, whose placement is unclear because it has been suggested to belong to the *P. occidentalis* group (Cole 1968) and the *P. californicus* group (Parker and Rissing 2002; Taber 1990).

Individuals were removed from the ethanol, then crushed in 100 µl 5% Chelex (in TE pH 8.0) and 1 µl proteinase K (5 mg/mL) was added. Samples were then

Table 1. Locale data (state: county, locale) for specimens in the genus *Pogonomyrmex* that were used to construct the mitochondrial phylogeny (see Figure 3). All locales are in the United States, except as noted.

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector and accession number
P. anzensis Cole				
CA: San Diego: Anza Borrego State Park, Split Mountain	33° 01′N	116° 07′N	260	SP Cover #4807
CA: San Diego: Borrego Mountains	33° 10′N	116° 10′N	240	SP Cover #4821
P. californicus (Buckley)				
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36° 36′N	118° 09′N	1540	RA Johnson #4127, 4128, 4132, 4133, 4134
CA: Inyo, Alabama Hills, 7.8 km S Jct Horseshoe Meadows & Whitney Portal Rds	36° 31′N	118° 06′N	1625	RA Johnson #4137, 4138
NV: Clark, 5.0 km E Jean	35° 46′N	115° 16′N	840	RA Johnson #4224
P. comanche Wheeler				
TX: Tarrant, Ft Worth Wildlife Refuge	32° 51′N	97° 28′N	180	AB Mayo #3985
P. magnacanthus Cole				
AZ: La Paz, 15.5 km E Tacna, Mohawk Dunes	32° 42′N	113° 47′N	140	RA Johnson #2235
CA: Riverside: Palm Desert, Bob Hope & Gerald Ford Dr	33° 47′N	116° 24′N	75	RA Johnson #1005
CA: San Diego: Anza Borrego, 8.0 km S Split Mtn	32° 59′N	116° 09′N	260	GC Snelling #98-052
P. maricopa Wheeler				
AZ: Pima, San Xavier Mission	32° 06′N	111° 00′W	770	CP Strehl #26
P. mohavensis Johnson				
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36° 36′N	118° 09′N	1540	RA Johnson #4129, 4130
CA: Inyo, Alabama Hills, 1.3 km S Jct Horseshoe Meadows & Whitney Portal Rds	36° 35′N	118° 07′N	1450	RA Johnson #4135, 4136, 4145, 4146
NV: Nye, Highway 374 at Rhyolite	36° 53′N	116° 49′N	1090	RA Johnson #4218
P. snellingi Taber				
Mexico: Baja California, 9.6 km N Guerrero Negro	28° 04′N	114° 01′W	5	RA Johnson #2663
Mexico: Baja California Sur, Vizcaino Desert	27° 47′N	113° 34′W	65	RA Johnson #3032

incubated at 57° C for 1 hour and subsequently heated to 95° C for 5 min, then centrifuged at 14,000 rpm for 10 min. The supernatant containing isolated DNA was then stored.

We amplified partial mitochondrial cytochrome oxidase I sequences using the LCO/HCO primers in a 25 µl reaction volume containing 0.01 units of Taq polymerase, 5 µl of 5× Go Taq Buffer, 1 µl $MgCl_2$ (50 mM), 1 µl dNTPs (10 mM), and 13.9 µl of H_2O. The locus was amplified using the following PCR program: an initial 4 min at 95° C, 38 cycles of 95° C for 30 sec, 45° C for 45 sec, and 68° C for 1.5 min, and finally 68° C for 4 min. PCR samples were purified using exonuclease I and shrimp acid phosphatase (ExoSAP-IT, USB Corporation, Cleveland, Ohio, USA) for digestion of single-stranded DNA (primers) and dNTPs. Samples were sent to the School of Life Sciences core DNA laboratory at Arizona State University and sequenced using an Applied Biosystems 3730 capillary sequencer.

Sequences were aligned using the autoalignment function in the program Sequencher version 4.6 (Gene Codes Corporation, Ann Arbor, MI). Phylogenetic trees were constructed with both neighbor-joining and maximum parsimony methods using the program Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0 (Tamura et al. 2007). Both analyses

were in complete agreement for all nodes and so the neighbor-joining tree was used in order to display branch lengths. Bootstrap values were calculated using 1000 pseudoreplicates and ten random taxon additions per replicate, then mapped onto the neighbor joining tree.

RESULTS

Pogonomyrmex mohavensis Johnson, n sp. (Figs 1A–E)

Worker description.—Head subquadrate (CI = 97.0–104.5), broadest just posterior to eye; posterior margin flat in full-face view. Longitudinal cephalic rugae prominent, in full-face view median rugae diverging only slightly towards the posterior corners of the head. In side view, rugae posterior to eyes not converging or forming circumocular whorls, but rather extending to vertex. Vertex rugose, with rugae often becoming weak or absent on posterior corners. Cephalic interrugal spaces slightly punctate, moderately to strongly shining. Anterior margin of clypeus flat to slightly concave. Mandible with six teeth, a seventh occasionally present as a denticle or very small tooth between the basal and subbasal teeth (76% had six teeth on both mandibles, 17% had an additional denticle on one mandible, 7% had an additional denticle on both mandibles, n = 98). Mandibular dorsum coarsely striated. MOD ranging from 0.21–0.24× HL. Eyes in profile situated slightly posterior to middle of head, OMD = 1.2–1.6 MOD. Antennal scapes relatively long (SI = 72–82), reaching to or surpassing vertex by less than the length of the basal funicular segment. Basal flange of scape flattened and very well-developed, at least partially translucent near margin. Psammophore well developed.

Mesosomal profile flattened to slightly convex. All mesosomal surfaces with prominent parallel/subparallel rugae. Dorsum of promesonotum with transverse rugae that curve obliquely to posterior on the pronotal sides, or rugae traverse obliquely from anterior to posterior. Mesopleura with transverse rugae angling posteriodorsally. Propodeum lacking spines or teeth, in side view evenly convex; rugae on propodeal dorsum transverse, posterior face of propodeum smooth and shining. Propodeal spiracles narrowly ovate. Interrugal spaces on mesosoma smooth and shining to slightly punctate and moderately shining. Legs moderately to strongly shining.

Petiolar peduncle long, ventral surface usually smooth, lacking tooth or lobe, occasionally with small angular process. In side view, petiolar node broadly but asymmetrically rounded with anterior surface notably shorter than posterior surface. Apex of node rounded, sometimes weakly angulate. In dorsal view, petiolar node longer than broad, widest anteriorly. Sides and dorsum of petiolar node moderately punctate, subshining, sculpture on dorsal surface variable: either lacking rugae, or with few transverse rugae, or up to several longitudinal rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest at or near posterior margin and tapering to anterior margin, maximal width about equal to length, moderately punctate, subshining. Gaster smooth and shining.

Erect whitish pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant semidecumbent hairs on funicular segments. Legs with moderately abundant suberect white setae. Mesosoma, petiole, and postpetiole with moderately dense erect to flexuous white setae, often similar in length, longest reaching to or slightly exceeding MOD; gastric tergites with more abundant, slightly shorter pilosity. Entire body concolorous ferruginous orange, or with gaster sometimes slightly lighter or darker than rest of body, but never black.

Worker measurements.—Holotype (paratypes, n = 12, notation: minimum-maximum). All measurements are in millime-

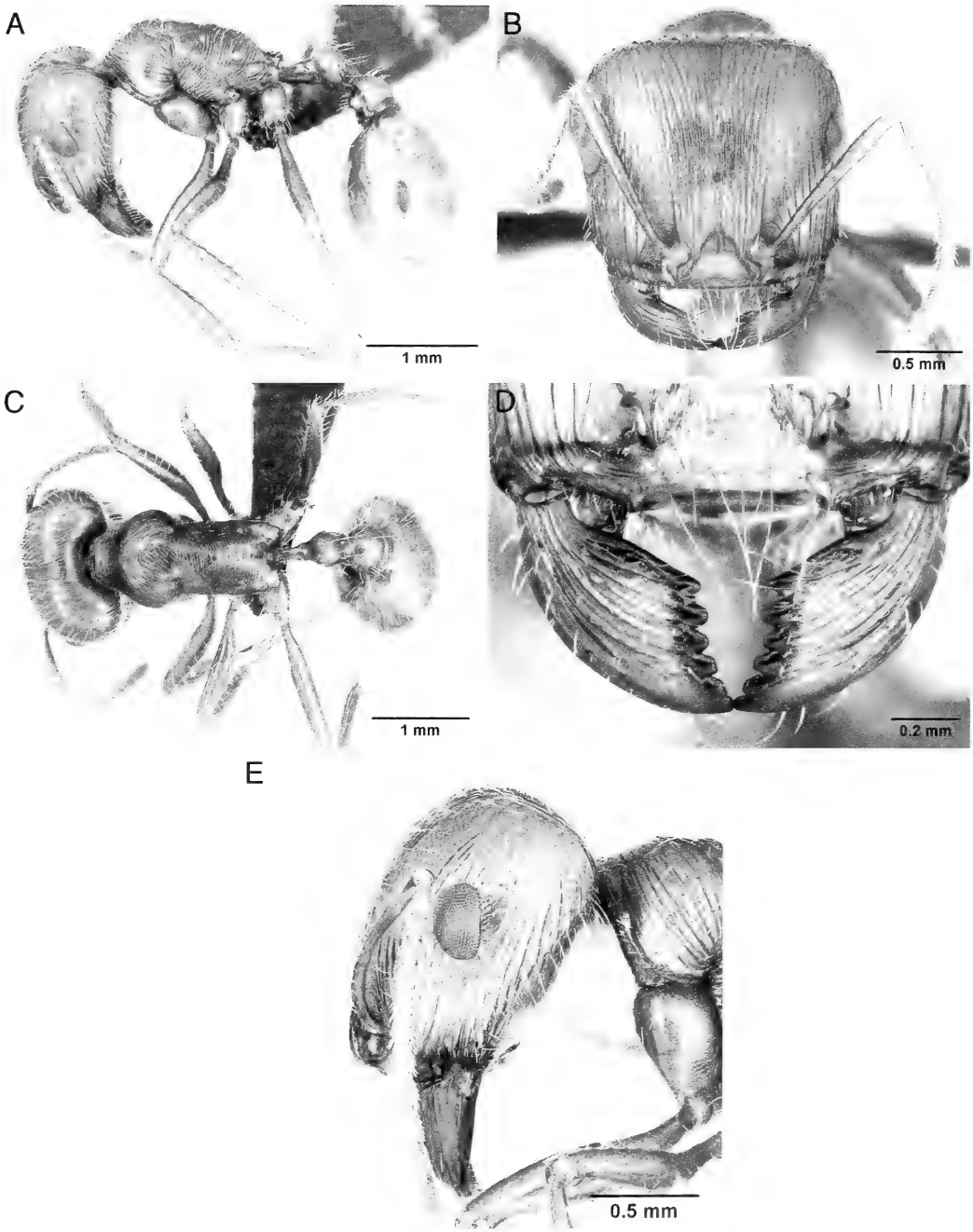


Fig. 1. *Pogonomyrmex mohavensis* Johnson – PARATYPE WORKER. **(A)** lateral view of worker body, **(B)** frontal view of worker head, **(C)** dorsal view of worker body, **(D)** frontal view of worker mandible with six teeth, plus a small denticle between the left basal and subbasal teeth, and **(E)** cephalic rugae extending to vertex, not forming circumocular whorls posterior to eyes.

ters. HL 1.56 (1.35–1.63); HW 1.61 (1.31–1.67); MOD 0.37 (0.30–0.37); OMD 0.46 (0.36–0.50); SL 1.14 (0.94–1.21); PNW 0.98 (0.85–1.04); HFL 1.65 (1.21–1.71); ML 1.90 (1.60–1.99); PW 0.40 (0.31–0.41); PPW 0.52 (0.45–0.56). Indices: SI 70.81 (70.06–81.75); CI 103.21 (97.04–104.55); OI 22.98 (20.95–24.82); HFI 102.48 (92.37–110.53).

Queen.—Unknown.

Male.—Unknown.

Diagnosis.—*P. mohavensis* is likely to be confused only with *P. californicus* but may be distinguished by the following characters: (1) *P. mohavensis* is slightly smaller (HW = 1.31–1.67) than sympatric *P. californicus* (HW = 1.22–1.78), (2) *P. mohavensis* has six mandibular teeth (a seventh sometimes occurs as a denticle between the basal and subbasal teeth), and (3) in side view, the cephalic rugae extend more or less directly to the vertex and do not converge posterior to the eyes or form circumocular whorls. In *P. californicus*, the mandible has seven more or less normally sized teeth and the cephalic rugae converge posterior to the eye, sometimes forming circumocular whorls. In addition, in some populations of *P. californicus* (including the population at the type locality of *P. mohavensis*) the gaster is dark brown to black. In *P. mohavensis*, the gaster is concolorous with the head and mesosoma, or sometimes a bit darker, but never dark brown to black.

In some specimens of both *P. californicus* and *P. mohavensis*, the cephalic rugae become weak or may even more or less disappear directly posterior to the eye, making evaluation of this sculptural character difficult, especially if magnification is low or the lighting is not good. In these cases, it appears that the number of mandibular teeth can secure separation. Even in examples of *P. mohavensis* with seven mandibular teeth, the extra tooth is much smaller than the flanking basal and subbasal teeth. This seventh tooth is fully developed in *P. californicus* and is subequal in size with the flanking teeth. Also note that substantial mandibular wear is common in older *Pogonomyrmex* workers, such that it is strongly recommended that at least several workers from each colony series be examined when attempting identification.

Type material.—Holotype (worker) plus 123 paratypes. **USA: *California***: *Inyo Co.*: Alabama Hills, 1.3 km S Junction Horseshoe Meadows & Whitney Portal Roads, 1450 m (36° 34.8'N 118° 7.1'W), 24 May 2008, leg. R.A. Johnson #4136. Nests were in mixed Mohavean Desert woody scrub habitat; dominant plant species included *Acamptopappus sphaerocephalus, Atriplex polycarpa, Atriplex canescens, Hymenoclea salsola, Grayia spinosa, Krascheninnikovia lanata, Eriogonoum fasciculatum, Coleogyne ramosissima, Ephedra* sp., *Gutierrezia* sp., *Lycium* sp., and *Cuscuta* sp. The holotype is deposited in the MCZ. Paratypes (n = 123 workers) all from the same locality and date as the holotype and leg. R.A. Johnson #4136 are distributed as follows: 3w CIDA, 9w CASC, 9w LACM, 15w MCZ, 9w UCDC, 12w USNM, 6w WPMC, 15w RAJC. Additional paratype series (RAJC) include RAJ #4135 (12w), #4145 (15w), and #4146 (24w); all series have additional workers in ethanol.

Additional material.—**USA: *California***: *Inyo Co.*: Alabama Hills at 7.5 km W Lone Pine, 1540 m, 23 May 2008 (36° 35.6'N 118° 8.5'W) (R.A. Johnson RAJ #4129, 15w; #4130, 6w; RAJC), Alabama Hills at 6.4 km W Lone Pine, 4950', 14 May 2006 (R.R. Snelling #06-007, 1w; RAJC), Artists Drive, Death Valley National Monument, 800 feet, 29 Apr. 1952 (CR-537, 9w; LACM). *Kern Co.*: 20 mi N Bakersfield, 5 Aug. 1959 (A.C. Cole CAL-345, 16w; LACM). ***Nevada:*** *Nye Co.*: Hwy 374 at Rhyolite, 1090 m, 18 Apr. 2009 (R.A. Johnson, RAJ #4218, 3w; RAJC), Rock Valley at 9 mi ENE Lathrop Wells, 14 Apr. 1970 (G. & J. Wheeler NEV-777, 3w; LACM). Figure 2 shows the known geographic distribution of *P. mohavensis*.

Etymology.—The specific epithet, *mohavensis*, is derived from this species occurring in the Mohave Desert.

Phylogenetic data

The mitochondrial phylogeny affirmed the taxonomic status of *P. mohavensis*, especially given that it is distantly related to sympatric colonies of *P. californicus*

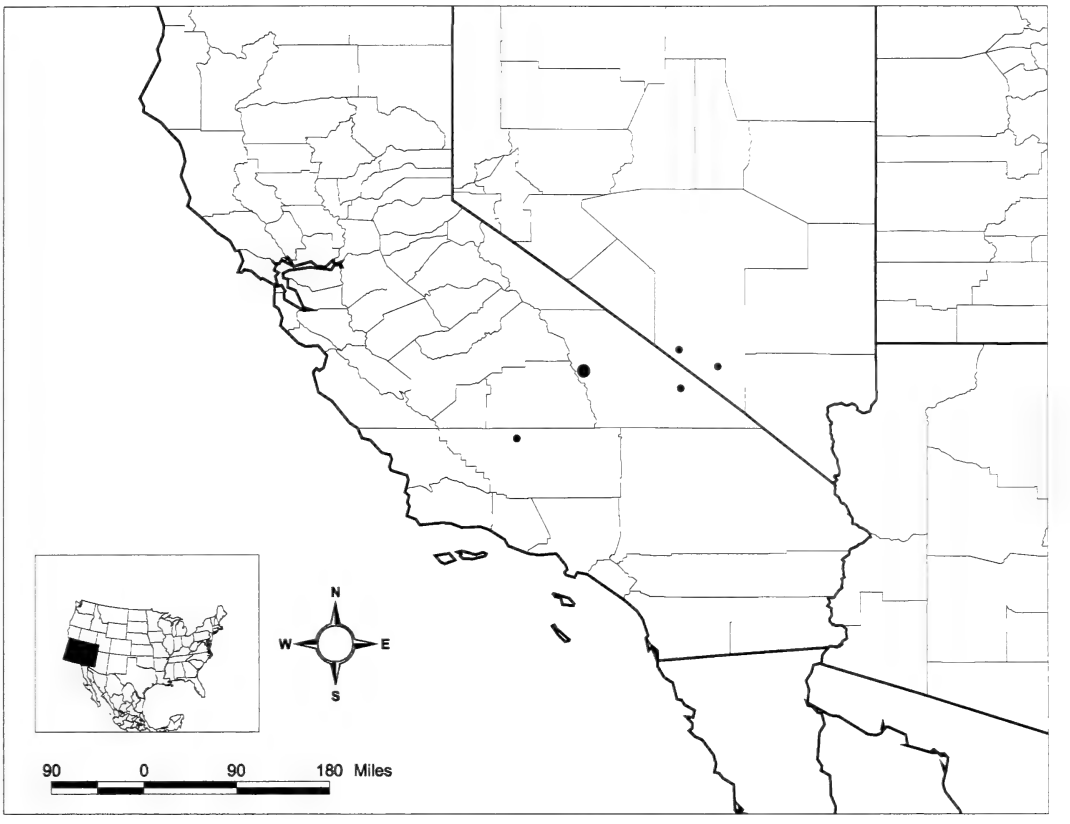


Fig. 2. Geographic distribution of *Pogonomyrmex mohavensis* Johnson; the type locality is denoted by the larger filled black circle.

(Figure 3). The phylogeny also inferred that *P. mohavensis* is most closely related to *P. snellingi*, which is endemic to the peninsula of Baja California, Mexico, and that *P. mohavensis*, *P. snellingi*, and *P. magnacanthus* comprise a clade of species that are restricted to hot desert habitats of North America. *Pogonomyrmex anzensis* was distantly related to other species in the *P. californicus* group, but we did not include any outgroup species, and thus could not determine if *P. anzensis* belongs in this species group (see also Parker and Rissing 2002). Overall, note that the phylogenetic relationships provided herein, as well as those in Parker and Rissing (2002) and Taber (1990, 1998), should be considered tentative. Better resolution of these species relationships requires a multiple gene phylogeny, which we are in the process of completing.

BIOLOGY AND DISCUSSION

The large series of workers collected during this study, combined with collections of sympatric *P. californicus* and a mitochondrial phylogeny of *P. mohavensis* and congeners in the *P. californicus* species group, make a formal description possible and confirm that *P. mohavensis* is a valid species. Based on dentition, *P. mohavensis* is not the undescribed species that has been known to exist for about twenty years and has been referred to by some authors as *Pogonomyrnmex* sp. B (Johnson 2000; Taber 1990, 1998); *P. mohavensis* has six teeth (this

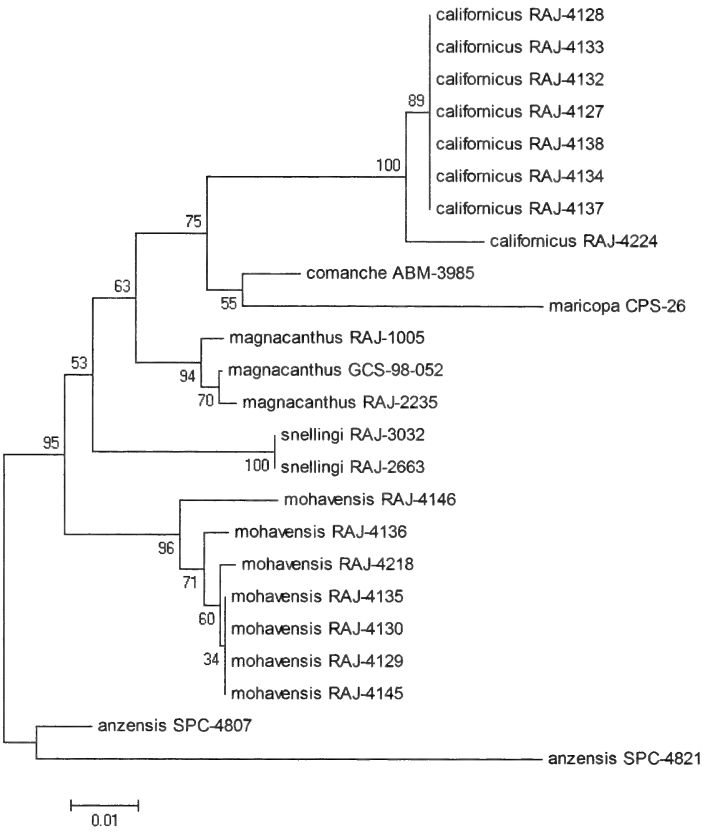


Fig. 3. Neighbor-joining tree for species in the *Pogonomyrmex californicus* group based on a 653 base-pair sequence of the cytochrome oxidase I gene. Numbers on branches represent bootstrap values based on 1000 pseudoreplications. The scale bar depicts expected rate of substitutions per site. Numbers following each species name refer to the accession number of the series from which the individual was taken; locale data for each series are given in Table 1.

study), whereas *P.* sp. B has seven teeth (Taber 1990, 1998).

Nests of *P. mohavensis* consist of a small circular tumulus that ranges from 7.5–13 cm in diameter; the shape is evenly symmetrical and lacks the crescentic shape typical of *P. californicus*. Nests were difficult to locate because of their low density and the small size of their tumulus; nests were most easily located by baiting foragers, then following them back to the nest. Nests were placed in various situations that included open exposed sites, under the edge of small bushes, and under dried cow dung. *Pogonomyrmex mohavensis* was sympatric with *P. californicus* at one site, and with *P. rugosus* at the other. Workers of *P. mohavensis* foraged solitarily during the day, harvesting seeds and related items. Partial excavation of nests indicated that colonies reach a maximum size of about 600–700 workers.

Males and females are unknown, but sexual larvae and pupae were excavated from multiple nests on 24 May, 2008, indicating that reproductive sexuals begin maturing by mid-June. Mating flights are predicted to be similar to those of *P. californicus*, in which flights are triggered by photoperiod (not rain-triggered as in most other species of *Pogonomyrmex*) (Johnson 2000) and likely take place over a 2–3 week period during early summer.

Current records suggest that *P. mohavensis* is restricted to areas in and near the Mohave Desert at elevations from 245–1540 meters (Figure 3). Three series of specimens found during this study were obtained by examining series of *P. californicus* (CASC, LACM, UCDC) because Roy Snelling had suggested that material of the new species had likely been misidentified as *P. californicus*. I also found one series of *P. mohavensis* that had been misidentified as *P. magnacanthus* (LACM). Moreover, *P. mohavensis* appears to be relatively uncommon compared to *P. californicus*.

KEY TO THE WORKERS IN THE *POGONOMYRMEX CALIFORNICUS* SPECIES GROUP FROM CENTRAL AND WESTERN NORTH AMERICA

(*P. anzensis* is included, though it may not belong in this species group).

1 Basal tooth strongly offset from basal margin; diastema present between basal and subbasal teeth, mandible sometimes with eight teeth when very small tooth occurs in diastema ..... ***snellingi***

– Basal tooth not strongly offset, lacking diastema between basal and subbasal teeth **2**

2(1) Dorsum of petiolar node, viewed from side, distinctly flattened, and viewed from above, with strong widely spaced wavy, subparallel, transverse rugae and usually distinct, broad, shallow, longitudinal depression; propodeum armed with short to long spines; cephalic interrugal punctures prominent ..... ***comanche***

– Dorsum of petiolar node, viewed from side, not flattened, and viewed from above, lacking strong, widely spaced, wavy, subparallel, transverse rugae and broad, shallow longitudinal depression; propodeal armature present or absent; cephalic interrugal punctures absent to prominent **3**

3(2) Eye unusually large (OI = 29–33), eye length slightly less than to notably more than oculo-mandibular distance (distance between lower margin of compound eye and nearest point of base of mandible); relatively small ant (4.7–5.2 mm) ..... ***magnacanthus***

– Eye small (OI = 18–24), eye length notably less than oculo-mandibular distance; usually larger ant (5.5–8.7 mm) **4**

4(3) Propodeal spines absent or with a pair of angles, denticles, or short to long spines; cephalic interrugal punctulation rather strong; interrugal punctulation of epipleura moderate to strong; interrugal spaces subopaque ..... ***maricopa***

– Propodeal spines absent; cephalic interrugal punctulation absent to moderate; interrugal punctulation of epipleura very weak or absent; interrugal spaces moderately to strongly shining **5**

5(4) Mandible with six teeth; posterior corners of head bearing a prominent longitudinal, strongly carinate ruga which is well set off from the outer portion of the occipital corner; in lateral view, ventral lobe of postpetiole with a strong triangular, ventral tooth ..... ***anzensis***

– Mandible with six or seven teeth; posterior corners of head lacking a prominent longitudinal ruga; in lateral view, ventral lobe of postpetiole lacking a ventral tooth **6**

6(5) Mandible always with seven teeth and cephalic rugae converging posterior to eyes in side view, often forming circumocular whorls ..... ***californicus***

– Mandible with six teeth, a seventh *small* tooth sometimes present between basal and subbasal teeth and the cephalic rugae extending to vertex in side view, not converging posterior to eyes or forming circumocular whorls ..... ***mohavensis***

ACKNOWLEDGMENTS

RAJ dedicates this paper to Roy Snelling, who provided specimens and locale information that facilitated locating colonies of *P. mohavensis*. I will always be indebted to Roy for his continued help, advice, and encouragement while I conducted research on *Pogonomyrmex*. I also thank Stefan Cover for comments that improved the manuscript, Brian Brown (LACM) and Brian Fisher (CASC) for the loan of specimens, and Brian Fisher for photographs.

LITERATURE CITED

Anderson, K. E., J. Gadau, B. M. Mott, R. A. Johnson, A. Altamirano, C. Strehl, and J. H. Fewell. 2006. Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology* 87: 2171–2184.

Bolton, B., G. A. Alpert, P. S. Ward, and P. Naskrecki. 2006. *Bolton's Catalogue of Ants of the World: 1758–2005*. Harvard University Press, Cambridge, Massachusetts.

Cole, A. C. 1968. *Pogonomyrmex Harvester Ants: A Study of the Genus in North America*. University of Tennessee Press, Knoxville.

Gadau, J., C. P. Strehl, J. Oettler, and B. Hölldobler. 2003. Determinants of intracolonial relatedness in *Pogonomyrmex rugosus* (Hymenoptera: Formicidae): mating frequency and brood raids. *Molecular Ecology* 12: 1931–1938.

Hölldobler, B. 1976a. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology* 1: 405–423.

———. 1976b. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology* 1: 3–44.

Johnson, R. A. 2000. Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology* 36: 89–122 + 83–88.

———. 2001. Biogeography and community structure of North American seed-harvester ants. *Annual Review of Entomology* 46: 1–29.

Lattke, J. E. 2006. A new species of *Pogonomyrmex* (Hymenoptera: Formicidae) from gallery forests of the Orinoco watershed, Venezuela. *Myrmecologische Nachrichten* 8: 53–57.

Parker, J. D. and S. W. Rissing. 2002. Molecular evidence for the origin of workerless social parasites in the ant genus *Pogonomyrmex*. *Evolution* 56: 2017–2028.

Taber, S. W. 1990. Cladistic phylogeny of the North American species complexes of *Pogonomyrmex* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 83: 307–316.

———. 1998. *The World of the Harvester Ants*. Texas A&M University Press, College Station.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24: 1596–1599.

Vásquez-Bolaños, M. and W. P. MacKay. 2004. Una especie nueva de la hormiga cosechadora del género *Pogonomyrmex* (Hymenoptera: Formicidae) de México. *Sociobiology* 44: 283–287.

J. HYM. RES.
Vol. 18(2), 2009, pp. 315–321

The Sexual Castes of *Pogonomyrmex anzensis* Cole (Hymenoptera: Formicidae)

ROY R. SNELLING†, GORDON C. SNELLING, JUSTIN O. SCHMIDT AND STEFAN P. COVER

(RRS) Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA, 90007, USA
(GCS) 13161 Rancherias Road, Apple Valley, CA 92308, USA; email: myrmecophile@armyants.org
(JOS) Southwestern Biological Institute, 1961 W. Brichta Dr, Tucson, AZ 85745, USA; email: ponerine@dakotacom.net
(SPC) Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA; email: scover@oeb.harvard.edu

Abstract.—The previously unknown sexual forms of the rare harvester ant, *Pogonomyrmex anzensis* Cole, were discovered at the type locality. They are here described and illustrated for the first time and the ecology of this species is discussed. Updated keys to the sexual forms of the California desert species of *Pogonomyrmex* are also presented.

Pogonomyrmex anzensis was described by Cole (1968) from a single series of workers collected by W. S. Creighton at Split Mountain, Anza-Borrego Desert State Park (ABDP), San Diego County, California. Several efforts were made to recollect this species by A. C. Cole, Jr., S. Taber (Taber 1998), R. R. Snelling, and others, to no avail. All such searches concentrated on the area of Split Mountain Wash, at a site that was presumably near the place where the type series was collected.

A further effort was undertaken in April 1997 by the team of S. P. Cover, R. A. Johnson, and G. C. Snelling (GCS). While previous searchers concentrated their efforts in the bed of the wash, this team began to investigate the steep rocky slopes on the south east side of the wash. Eventually, a few foraging workers were found and followed back to their nest under a moderate-sized stone. *P. anzensis* was easily recognizable in the field because the mandibles of the workers have only six teeth. The other two *Pogonomyrmex* species in the immediate area (*P. californicus* and *P. magnacanthus*) both have seven mandibular teeth. Several other *P. anzensis* colonies were found at the Split Mountain site, all living on steep, extremely rocky slopes. This initial success gave us a better notion of how to search for the species. This species was eventually found at several other sites in Anza-Borrego Park (see below). A return visit by GCS in the following year resulted in the discovery of the sexual forms in one nest. These are described below.

TERMINOLOGY

All measurements were made from mounted, fully dry, specimens under a binocular microscope with 15× oculars, fitted with an ocular micrometer. In the descriptions, the following acronyms are used:

CI	(HW) (100/HL).
EL	Maximum length of compound eye in lateral view.
EW	Maximum width of compound eye in lateral view.
HL	With head in full face view, the maximum length from ante-

†Deceased

riormost margin of clypeus (the thin lamelliform clypeal apron) to posterior margin.

HW — With head in full face view, the maximum width, exclusive of compound eyes.

IOD — The minimum distance between the inner margins of the posterior ocelli.

ML — Length of mandible, measured from articulation with head to greatest distance from articulation, regardless of any curvature.

OD — The transverse diameter of the anterior ocellus.

OI — (EL) (100/HL).

OMD — The distance between the lower margin of the compound eye and the base of the mandible, measured in lateral view.

OOD — The minimum distance between the outer margin of a posterior ocellus and the adjacent inner margin of the compound eye.

OVD — With the head in frontal view, the shortest distance between either posterior ocellus and the posterior margin (see below)

PW — Maximum width of pronotum in dorsal view.

SI — (SL) (100/HL).

SL — Maximum length of scape, exclusive of basal condyle.

WL — Diagonal length of mesosoma in profile, from anterior declivity of pronotum (exclusive of pronotal "neck") to apex of metapleural lobe.

Pogonomyrmex anzensis Cole

Pogonomyrmex (*P.*) *anzensis* Cole 1968:84, 7–89; pl. III fig. 13 pl. IV fig. 11; pl. VI fig. 12; pl. VII fig. 15; Taber 1998:101, 140, 149, 165.

Male

Diagnosis.—Mandible with four teeth on strongly oblique cutting margin; propodeum evenly curved to broadly subangulate in profile; gastral tergum 1 (abdominal tergum 4) with no pilosity visible in profile and in dorsal view with only sparse, inconspicuous short, straight hairs.

Measurements (mm) (n = 10). HL 1.37; HW 1.50; SL 0.93; EL 0.47; EW 0.33; OMD 0.20; WL 2.45; TL ca. 7.20. Indices. CI 109; SI 62; OI 31.

Description.—Mandible with four teeth on strongly oblique masticatory margin (Fig. 6); tip of subbasal tooth sometimes weakly bifid; basal tooth not offset. Anterior margin of clypeus broadly and shallowly concave. Scape long, in repose nearly attaining level of posterior margin as seen in full frontal view. Pilosity suberect to erect, long hairs of vertex mostly straight, longest slightly curled apicad, not much, if any, exceeding eye width; scape hairs all short and decumbent, all shorter than minimum scape width. Cephalic rugae fine and close, slightly wavy, interspaces weakly punctate and moderately shiny.

In profile, anterior face of pronotal collar straight and oblique. Anterior face of mesonotum straight and not overhanging pronotum, about one-half as long as dorsal surface. Propodeum evenly curved to broadly subangulate in profile, without spines or denticles. Side of pronotal collar with fine superficial rugulae, especially laterad; mesepisternum with fine irregular, mainly longitudinal rugulae and superficially shagreened; mesonotum shiny between scattered coarse piligerous punctures; propodeum mostly with fine close punctures, but with variable smooth shiny areas, especially mesially. Tibiae with suberect hairs that are much shorter than tibial width.

Petiole without anteroventral process; node rounded in profile, broadly and evenly rounded into anterior peduncle; venter glabrous. Postpetiole node low and broadly rounded, anterior slope about three times as long as posterior slope.

Disc of gastral tergum 1 (abdominal tergum 4) smooth, shiny and impunctate; following segments similar but with scat-

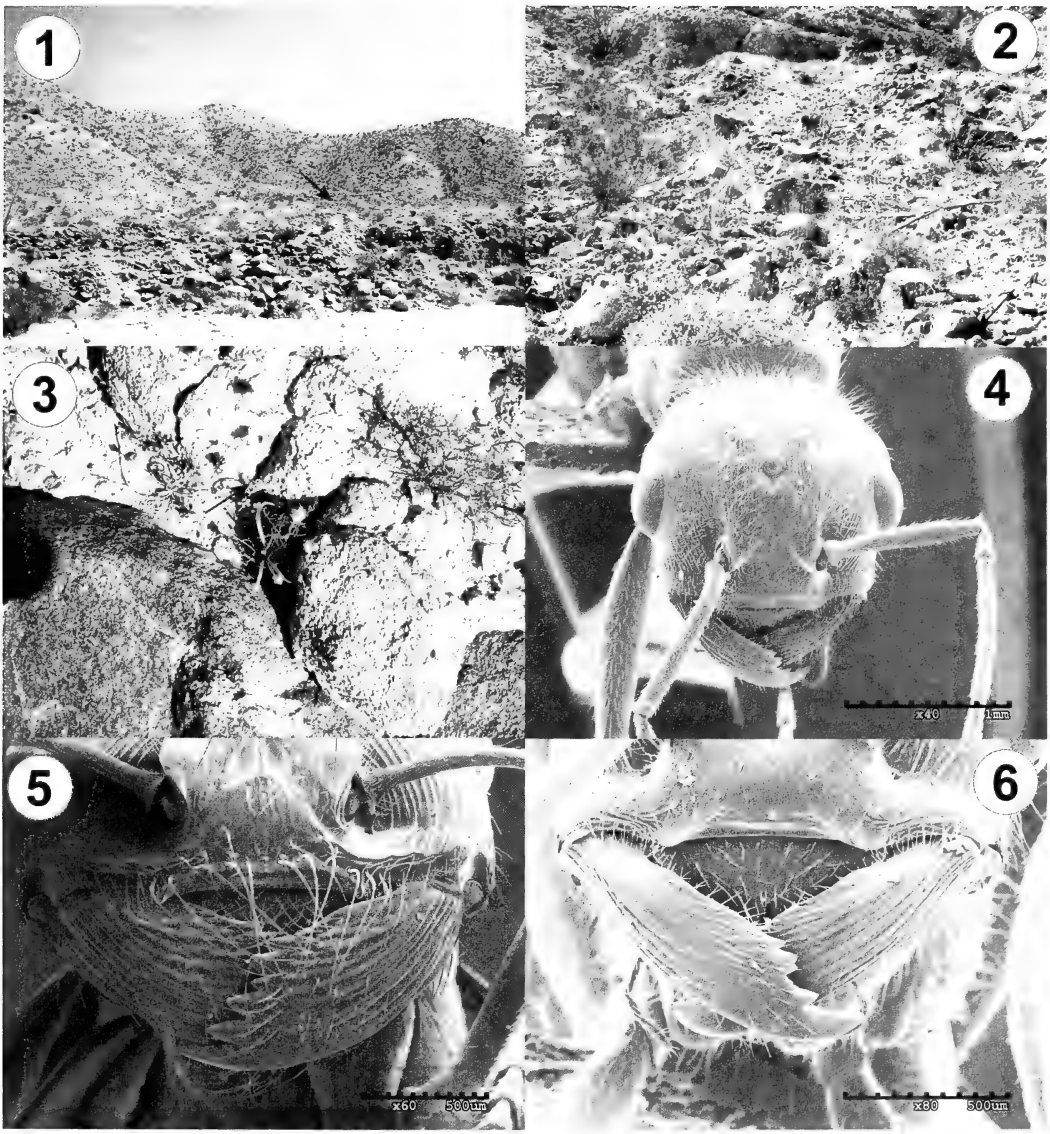


Fig. 1. Habitat of *Pogonomyrmex anzensis* at the type locality of Split Mountain; arrow indicates location of colony.
Fig. 2. Habitat immediately surrounding a *P. anzensis* colony at the type locality; arrow in lower right corner indicates nest entrance.
Fig. 3. Nest entrance hole (indicated by arrow) of *P. anzensis* colony at the type locality.
Fig. 4. Head of male *P. anzensis*.
Fig. 5. Mandibles of female alate *P. anzensis*.
Fig. 6. Mandibles of male *P. anzensis*.

tered minute piligerous punctures. Tergum 1 largely bare, with sparse short hairs basad on each side; following segments with sparse short and medium-length hairs, especially at segment margins; sterna only slightly more pilose, second segment with short straight hairs on disc.

Queen

Diagnosis.—Mandible with six teeth on oblique cutting margin, sometimes with

small subbasal tooth or denticle. Mesoscutum prominent in side view, forming broadly rounded, anterodorsally projecting dome that does not protrude over the pronotum, sculpture absent except for scattered coarse punctures and faint traces of longitudinal striae visible on parts of the dorsal surface, pubesence absent. Ventral surface of postpetiole with well-developed tooth.

Measurements (mm) (n = 1). HL 1.79; HW 1.87; SL 1.33; EL 0.41; EW 0.31; OMD 0.53; WL 2.44; TL ca. 6.80. Indices. CI 104; SI 74; OI 23.

Description.—Small, scarcely larger than large conspecific workers. Mandibles as described above, dorsal surfaces coarsely striate, strongly shining. Head in full-face view slightly broader than long, posterior corners abruptly rounded, almost angulate, posterior margin flat. Dorsum and sides of head conspicuously rugose, in side view rugae forming circumocular whorls posterior to the eye, interrugular spaces smooth and strongly shining. Antennal scape short, failing to reach the posterior margin by at least twice its maximum diameter. Psammophore well-developed. Mesoscutum as described above. Most of pronotum smooth and shining, but with several strong rugae that extend from the lower pronotal sides to nearly the midline on the pronotal collar. Katepisternum finely rugulose, interrugal spaces roughed, less shiny than those on most of the rest of the mesosoma, some coarse, decumbent pubesence present at least on the posterior surfaces, weakly to moderately shining. Propodeum unarmed, rounded to subangulate, sides and dorsal surface rugose, shining, posterior surface smooth and strongly shining. Petiole without anteroventral process, ventral surface glabrous. In side view, node with moderately sharp apex, posterior surface slightly convex, weakly rugulose, interrugular spaces roughened and only moderately shiny. Postpetiole in side view with low, rounded node, a small anterior-facing denticle just ventral to the petiolar articulation, and a well-developed ventral tooth. Gastric tergites smooth and shining, with weak tessellated microscuplture, and scattered coarse setae-bearing punctures. Body surfaces in general with moderately abundant coarse erect to suberect setae.

Specimens examined.—CALIFORNIA, San Diego Co.: Split Mountain, ABDP, 22 Apr. 1952 (W. S. Creighton; LACM, MCZC, USNM); 1.7 mi S jct. Split Mtn. Rd. and Fish Creek Rd., ABDP, 33.02°N 116.10°W, 500 ft., 2 Apr. 1997 (G. C. Snelling, S. Cover, R. Johnson; GCSC, LACM, MCZC, RAJC); Split Mountain, ABDP, 33.01°N 116.10 °W, 500 ft., 26 Apr. 1998 (G. C. Snelling; GCSC, LACM); Ocotillo Wells Vehicular Recreation Area, ABDP, 33.13°N, 116.13°W, 2 Apr. 1997 (G. C. Snelling S. Cover, R. Johnson; GCSC, LACM, MCZC, RAJC); same except 28 Feb. 1998 (G. C. Snelling 98-005, and R. R. Snelling 98-005; GCSC, LACM); Henderson Rd. and Pegleg Rd., 33.28°N 116.30°W, 26 Apr. 1998 (G. C. Snelling 98-051; LACM), fragments ex unknown spider web under rock.

RESULTS AND DISCUSSION

Although known only from a few collections made in the Anza Borrego Desert State Park and immediate surrounding areas, this species will no doubt be found in other suitable habitats in western Imperial, Riverside and eastern San Diego Counties. Although this species will likely be found in other Southern California localities we feel that it may be a predominantly Mexican species which is at the northern limit of its range in California. Within the approximately 940 sq mile park this decidedly rare ant is known from only three locations. All are on relatively steep, extremely rocky, west to southwest facing slopes. It is unknown at this time if this slope preference is real or if it is an artifact of inadequate collecting. Of the three sites, the Pegleg location is the most comparable to the nesting sites of the other *Pogonomyrmex* species. At this location the hillside is much less severe than the other two sites,

being less steep and rocky. However it still does fall within the parameters we have concluded are integral for the survival of this ant species.

According to Creighton's field notes, the type nest at Split Mountain was found in gravelly soil located under a large, partly buried boulder. The entrance was obscure and to one side of the boulder. One hundred seventy workers were taken. Based on this description, subsequent collectors have concluded that the type colony was found in or at the edge of the wash. If this interpretation of his notes is correct, then this is an atypical nesting situation for this species. Thus far all other collections are from rocky hillsides in cactus scrub (Figs 1–2). The only other *Pogonomyrmex* species in California that sometimes occur in this habitat type are *P. tenuispina* Forel and *P. rugosus* Emery. However, neither of these species exhibits a preference for nest sites as steep and rocky as those of *P. anzensis*. Nest entrances are typically unmarked by a crater, although on occasion there may be a small dispersed amount of chaff or soil, barely discernable from the surrounding litter on the ground. Nest entrances are usually, but not always, situated adjacent to a large rock (Fig. 3). During the course of collecting, a few colonies were located in which the nest entrance was just a simple hole in the soil. Workers forage singly and are slow-moving and timid. Workers were noted often to tuck their gasters under the mesosoma when foraging. The ants make little effort to defend the nest when disturbed other than running around somewhat excitedly, then retreating. Although there are several other harvester ants in the general area, (*Pogonomyrmex californicus* Buckley, *P. magnacanthus* Cole, *P. rugosus* and *Messor pergandei* Mayr), these species all nest and forage primarily in the wash and on the lower hillsides. By nesting in these extreme habitats, *P. anzensis* avoids most of the foraging competition from other harvester ant species in the area. *M. pergandei* will often forage onto the hillside but generally at times of the day when *P. anzensis* is not active. Other ants occurring with *P. anzensis* on the hillside are *Pheidole hyatti* Emery, *Pogonomyrmex imberbiculus* Wheeler and a large diurnal *Myrmecocystus* species, most likely *M. mendax* Wheeler, a common inhabitant of rocky localities in Southern California.

Kangaroo rats, *Dipodomys* spp., are known to frequently raid the seed caches of granivorous ants such as *Pheidole* spp. that store their seeds in shallow chambers of the nest. These rodents are thought to be capable of detecting the clumped seed resources by olfaction (Reichman and Oberstein 1977). It is not known if these rodents impact *Pogonomyrmex anzensis* colonies in search of seeds; however the rocky nature of the soil and depth at which the seeds are stored must make such rodent excavations nearly as hard for them as it is for mere humans.

Little is known about the foraging preferences of this ant species. However it is presumably a generalized seed collector and scavenger like its congeners. Dominant plants on the hillside at the type locality are creosote bush (*Larrea tridentata* (Sesse & Moc ex DC.) Coville), Brittlebush (*Encelia farinosa* Torrey and Gray) and ocotillo (*Fouquieria splendens* Engelm.). During the spring if adequate rain has fallen, the hillside is dotted with the numerous annuals that take advantage of the moisture to flower and set seed.

At the Ocotillo Wells site, foragers were observed to be collecting small pieces of the leaves of *Encelia farinose*. It is very unlikely that this is a preferred food source and we have never seen any other ants collecting leaf bits from this plant. This behavior indicates to us that overall resources were very scarce that season, and that these ants are fairly adaptable relative to what they might consume.

KEYS TO THE SEXUAL FORMS OF CALIFORNIA DESERT *POGONOMYRMEX*

Queens

1 Venter of petiole with several erect hairs, usually long; scape notably shorter than distance from mandible base to corner of vertex; forewing usually with one cubital cell 2
– Venter of petiole without erect hairs; scape usually at least as long as distance from mandible base to corner of vertex; forewing usually with two cubital cells 4
2(1) Frons uniformly longitudinally rugulose or striate between eye and midline; dorsum of petiolar node without longitudinal furrow; HW at least 1.9 mm, usually more than 2.2 mm 3
– Frons weakly longitudinally striate in middle, closely punctulate on either side; dorsum of petiolar node with longitudinal furrow dividing summit of node; HW no more than 1.8 mm ..... ***colei* Snelling**
3(2) Cephalic and mesoscutal rugae fine and closely spaced, producing a silky luster; outer surface of scape base, in repose, not strongly concave; less than 10 mm long ..... ***desertorum* Wheeler**
– Cephalic and mesoscutal rugae coarse and widely spaced, not producing a silky luster; outer surface of scape base, in repose, strongly concave; more than 11 mm long ..... ***rugosus* Emery**
4(1) Mandible with seven teeth, basal tooth larger than subbasal tooth; petiole and postpetiole without prominent ventral processes; lateral angle of vertex not carinate 5
– Mandible with six teeth, basal tooth smaller than subbasal tooth (Fig. 5); petiole and postpetiole each with prominent ventral process; lateral angle of vertex with sharp, short carina ..... ***anzensis* Cole**
5(4) In profile, cephalic rugae forming concentric loops over eye; propodeum generally unarmed, rarely with short denticles 6
– In profile, cephalic rugae not forming concentric loops over eye; propodeum distinctly bispinose ..... ***subnitidus* Emery**
6(5) Eye small, OI 21–24; OMD nearly twice EL 7
– Eye large, OI 31; OMD no more than EL ..... ***magnacanthus* Cole**
7(6) Interrugal spaces of head smooth and shiny, without definite sculpture; propodeum unarmed ..... ***californicus* (Buckley)**
– Interrugal spaces of head moderately shiny, with weak to moderate sculpture; propodeum generally unarmed, but sometimes bituberculate ..... ***maricopa* Wheeler**

Males

1 Venter of petiole with numerous long, erect, ventrally directed hairs; forewing usually with one cubital cell; head, in frontal view, with margin between eye and vertex corner evenly, rather strongly, convex 2
– Venter of petiole usually with no erect hairs, rarely 1–3 present; forewing usually with two cubital cells; head, in frontal view, not evenly or strongly convex between eye and vertex corner 4
2(1) Outer surface of base of antennal scape strongly flattened or broadly concave; body color generally fuscous yellow or brown 3
– Outer surface of base of antennal scape neither flattened nor concave; petiole, postpetiole and gaster lighter colored than head and mesosoma ..... ***desertorum* Wheeler**
3(2) Large, HW at least 2.1 mm; hairs abundant, long, flexous, pale; node of petiole, in profile, low, broadly rounded ..... ***rugosus* Emery**

– Smaller, HW about 1.5 mm; hairs straight and stiff, with blunt tips, yellowish; node of petiole, in profile, high and sharply rounded at summit ..... ***colei* Snelling**

4(1) Denticulate margin of mandible transverse, with 2 to 5 teeth; vertex usually without sharply elevated longitudinal ridge; apex of paramere, in profile, angulate with lower margin 5

– Denticulate margin of mandible oblique, with 4 or 5 teeth; vertex usually with sharply elevated median longitudinal ridge; apex of paramere, in profile, broadly rounded into lower margin 7

5(4) Eye small, OI 32–43; OMD more than 0.33 × EL 6

– Eye large, OI 52–54; OMD equal to, or less than, 0.33 × EL ..... ***magnacanthus* Cole**

6(5) Mandible with 2–4 (usually 2 or 3) teeth; anterior declivity of pronotum, in profile, straight, meeting collar at abrupt angle; length and width of terminal lobe of paramere, in profile, subequal ..... ***californicus* (Buckley)**

– Mandible with 3–5 (usually 3 or 4) teeth; anterior declivity of pronotum, in profile, concave, meeting collar at well rounded angle; terminal lobe of paramere, in profile, broader than long ..... ***maricopa* Wheeler**

7(4) Anterior declivity of pronotum long and not concave in profile; anterior declivity of mesoscutum short in profile; mandible slender and parallel-sided, apical tooth conspicuously longer than remaining teeth (Figs. 4, 6) ..... ***anzensis* Cole**

– Anterior declivity of pronotum short and strongly concave in profile; mesoscutum massive and with long anterior declivity; mandible broader, not parallel-sided, apical tooth shorter ..... ***subnitidus* Emery**

ACKNOWLEDGMENTS

We thank Kelly Pinion and the staff of Anza Borrego Desert State park for their helpful logistical support and the permits for the study in the park, Giar-Ann Kung, LACM for her able and top-notch work to make the SEM images, and Bill Savary for assisting in final preparation of the figures.

LITERATURE CITED

Cole, A. C., Jr. 1968. *Pogonomyrmex* harvester ants. A study of the genus in North America: Knoxville, TN. 222 pp.

Reichman, O. J. and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. *Ecology* 58: 636–643.

Taber, S. 1998. *The World of the Harvester Ants*. College Station, TX. 231 pp.

J. HYM. RES.
Vol. 18(2), 2009, pp. 322–325

Pogonomyrmex anzensis Cole: Does an Unusual Harvester Ant Species Have an Unusual Venom?

JUSTIN O. SCHMIDT AND GORDON C. SNELLING

(JOS) Southwestern Biological Institute, 1961 W. Brichta Dr., Tucson, AZ 85745, USA;
email: ponerine@dakotacom.net
(GCS) 13161 Rancherias Road, Apple Valley, CA 92308, U.S.A.;
email: myrmecophile@armyants.org

Abstract.—*Pogonomyrmex anzensis* was a lost "mystery" ant not seen or collected for 45 years after its original single collection, despite intense search by some of the finest myrmecologists of the time. Its rediscovery by a team in 1997 revealed the species nested in hard rocky hillside slopes that are exceptionally sun-baked, hot, and dry. Since these ants live under unusually extreme conditions compared to other members of the genus, we wondered if their unusual biological circumstances also translated into unusual venom. Compared to the venoms of most other species of *Pogonomyrmex*, the venom of *P. anzensis* is exceptionally lethal to mammals, but the amount of venom produced is low. The defensive behavior of *P. anzensis* reflects these venom properties: worker ants are unaggressive compared to other *Pogonomyrmex* spp. and their stings induce little pain or reaction in humans. Overall, *P. anzensis* is an atypical harvester ant species both in its habitat and behavior and in its reduction of venom production. The reduced venom production is likely a response to the combination of harsh conditions and an environment essentially free of vertebrate predators.

Key words.—*Pogonomyrmex*, *anzensis*, venom, lethality

Harvester ants in the genus *Pogonomyrmex* are among the most conspicuous arthropods within their habitats (Cole 1968; Taber 1998) and are famous for their exceedingly painful and long lasting stings (Schmidt and Blum 1978). Their venoms are among the most toxic of arthropod venoms, having lethalities many times greater than honey bees, most other stinging wasps and ants, and spiders and scorpions (Schmidt 1990). Harvester ant venom is used primarily for defense against large predators, and, with the exception of horned lizards in the genus *Phyrnosoma*, worker *Pogonomyrmex* spp. have no major vertebrate predators (Schmidt and Schmidt 1989). This apparent freedom from vertebrate predation leads one to wonder if predatory pressure by vertebrates on ancestral *Pogonomyrmex* species was responsible for the incredible painfulness and lethality of harvester ant venoms and for maintaining that activity.

Pogonomyrmex anzensis lives in small, sporadic colonies in harsh desert rocky slopes around Anza Borrego in California, USA (Snelling et al. 2009). The ants are exceedingly timid, do not sting readily, are apparently allopatric to *Phrynosoma*. Thus, *P. anzensis* represents an interesting example of an unusual harvester ant species living in an extreme habitat free from even horned lizard predators. The goal of the research reported here was to determine if these conditions led to a loss of defensiveness and venom activity in *P. anzensis*.

MATERIALS AND METHODS

Pogonomyrmex anzensis workers were collected from two locations in Split Mountain, Anza-Borrego Desert State Park, San

Diego County, California: 2.7 km. S of jct. Split Mtn. Rd. and Fish Creek Rd., 33.02°N 116.10°W, 152 m, 2 April 1997, and at Split Mountain, 33.01°N 116.10 °W, 152 m, 26 April 1998; *P. wheeleri* Olsen were collected 18 km E. of jct. Mex. Hwys. 40 and 15 on Mex. 40, Mazatlan, Sinaloa, Mexico, 7 July, 1983; *Apis mellifera* L. were collected as foragers entering and leaving a feral colony near Cañas, Guanacaste, Costa Rica, 5 February 1987. Live ants were frozen and maintained at −26°C until dissected; the bees were treated similarly except the frozen conditions were −10°C. Pure venom was obtained from the frozen ants by the method of Schmidt (1995). In brief, a sting apparatus from a frozen ant was removed to a spot of distilled water, the venom reservoir (minus filamentous glands) was pinched off and removed from the rest of the sting apparatus, rinsed with distilled water, and placed in clean distilled water. Collected reservoirs were pooled in a single water drop, after which the venom was squeezed from each torn reservoir with pairs of forceps and the empty chitinous reservoirs were combined for weighing. The pure venom was lyophilized and stored at −26 °C until used.

Swiss white mice were used for lethality analyses and were provided food and water ad lib throughout the experiments. Venom was dissolved in 0.15 M saline and volumes of 0.6% of the mouse body weight were injected intravenously into groups of 6 (ants) or 8 (bees) mice. LD_{50} values (24 hr) were calculated according to the method of Reed and Muensch (1938) with 95% confidence intervals (CI) determined by the method of Pizzi (1950). The total lethal activity of the venom from single ants was expressed as the lethal capacity calculated by dividing the weight of venom per individual ant by the LD_{50} (Schmidt 1986). LC is expressed in terms of weight of mouse that would receive a median lethal dose of venom from the sting of one average ant.

RESULTS

Workers ants of *P. anzensis* are retiring and timid compared to other species in the genus. They make little effort to defend the nest when disturbed, and mainly run around erratically and excitedly before retreating. They also are hesitant to sting; in fact, so hesitant that the only stings (n = 3) received were those experienced by one of us (GCS) when individuals were pressed against the skin. The subsequent pain and reaction was milder and less severe than that experienced when stung by most other species of *Pogonomyrmex*. As seen under a dissecting microscope, venom reservoirs of *P. anzensis* often appeared collapsed or partially collapsed and only half filled or less with venom. Of 38 reservoirs scored, seven appeared empty, 11 one quarter full, 19 one half full and only one mostly full. The low filling of venom in the reservoirs corresponded to the low amount of dried venom per reservoir (Table 1). Another indication of low venom production and quantity in the species is the ratio of weight tissue in empty reservoirs to the venom within the reservoirs. The amount of venom per reservoir in *P. anzensis* was about 10% as much as for the congeneric *P. wheeleri*, whereas the ratio of empty reservoir tissue was roughly 10 times as much (Table 1). Virtually all other species of *Pogonomyrmex* exhibit venom to empty reservoir ratios similar to those of *P. wheeleri* (personal observations, JOS). Africanized ("killer") honey bees were chosen as a comparison outgroup. Their venom to empty reservoir ratio is similar to that of *P. wheeleri*.

The lethality of the venom of *P. anzensis* to the mouse vertebrate model is shown in Table 2. The venom itself is strongly lethal, exhibiting an LD_{50} of 0.20 mg/kg, three times more lethal than the venom of *P. wheeleri* or many other *Pogonomyrmex* species (unpublished data, JOS), and 10 times more lethal than that of the honey bee. A more realistic measure of venom effective-

Table 1. Quantity of venom in *Pogonomyrmex anzensis* and reference stinging Aculeata.

Taxon (location)	Material	n	Weight/insect (µg)	Empties/Venom
Pogonomyrmex anzensis	Venom	31	4.08	
(Split Mt Rd & Fish Cr.)	Empty reservoirs*	31	1.61	.395
(Split Mountain)	Venom	100	4.75	
	Empty reservoirs	89	1.24	.261
Pogonomyrmex wheeleri	Venom	41	46.2	
	Empty reservoirs	601	1.81	.039
A. mellifera (Africanized)	Venom	51	156	
	Empty reservoirs	51	13.7	.088

* Empty reservoirs consist of reservoir tissue with traces of residual venom

ness is lethal capacity, a measure of the killing power in terms of grams of animal that would receive a LD_{50} dose of venom if all of the venom in one individual were delivered in a sting. By this measure, a *P. anzensis* sting is less than one third as potent as one from *P. wheeleri* and less than half that of a honey bee.

DISCUSSION

For a harvester ant, the sting of *P. anzensis* is exceptionally mild to humans, with stings resulting in little more than mild pain and a small reddened area. The exceeding lethality of the venom itself indicates that the species has retained the ancestral venom activity observed throughout the genus. We do not have a species level phylogeny including *P. anzensis* and, therefore, cannot compare its venom activity to that of sibling species. In contrast to the extreme lethality of the venom, *P. anzensis* workers produce very little venom. Evidence for this is two-fold: the venom amount is small; and the reservoir that stores the venom is large and has the capacity to contain much more venom. A consequence of the combined lethality and low quantity of venom produced is a relatively low venom lethal capacity. These findings concur with field observations that the ants do not strongly defend themselves or their colonies and that their stings are not particularly effective as a potential deterrent to vertebrate predators.

Selection pressure can act on organisms living in harsh environments such as *P. anzensis* by either changing the nature of the venom itself, or by altering the control of venom production. We suggest that the evolutionarily more rapid and efficient

Table 2. Lethality and lethal capacities to mice of *Pogonomyrmex anzensis* venom and venoms of reference stinging Aculeata.

Taxon (location)	LD_{50} (mg/kg) (95% CI)	µg Venom	Lethal capacity insect (g mouse/sting)
Pogonomyrmex anzensis			
(Split Mt Rd & Fish Cr.)	.22	4.08	18.5
(Split Mountain)	.18	4.75	26.4
*Pogonomyrmex wheeleri** (Mazatlan, Mexico)	.60 (.38–.96)	46.2	77.0
A. mellifera (Africanized)** (Cañas, Costa Rica)	2.8 (2.0–4.1)	156	55

* Data from Schmidt and Schmidt (1985)
** Data from Schmidt (1995)

means of adapting to a harsh, essentially predator-free environment is to restrict investment of valuable energy and resources in venom production by limiting venom synthesis – something apparently occurring in *P. anzensis*.

ACKNOWLEDGMENTS

We thank Kelly Pinion and the staff of Anza-Borrego Desert State Park for logistical support and permits, and Rick Vetter for review of the manuscript.

LITERATURE CITED

Cole, A. C., Jr. 1968. *Pogonomyrmex Harvester Ants: A Study of the Genus in North America*. University of Tennessee Press, Knoxville, Tennessee. 222 pp.

Pizzi, M. 1950. Sampling variation of the fifty per cent end-point, determined by the Reed-Muench (Behrens) method. *Human Biology* 22: 151–190.

Reed, L. J. and H. Muench. 1938. A simple method of estimating fifty per cent endpoints. *American Journal of Hygiene* 27: 493–497.

Schmidt, J. O. 1986. Chemistry, pharmacology and chemical ecology of ant venoms. Pp. 425–508 *in* Piek, T., ed. *Venoms of the Hymenoptera*. Academic Press, London. 570 pp.

———. 1990. Hymenopteran venoms: striving toward the ultimate defense against vertebrates. Pp. 387–419 *in* Evans, D. L. and J. O. Schmidt, eds. *Insect Defense: Adaptations and Strategies of Prey and Predators*. State University of New York Press, Albany, New York. 482 pp.

———. 1995. Toxinology of venoms from the honeybee genus *Apis*. *Toxicon* 33: 917–27.

——— and M. S. Blum. 1978. A harvester ant venom: chemistry and pharmacology. *Science* 200: 1064–66.

Schmidt, P. J. and J. O. Schmidt. 1985. Queen versus worker venoms: are they equally lethal? *Toxicon* 23: 38–39.

——— and J. O. Schmidt. 1989. Harvester ants and horned lizards: predator-prey interactions. Pp. 25–51 *in* Schmidt, J. O., ed. *Special Biotic Relationships in the Arid Southwest*. University of New Mexico Press, Albuquerque, New Mexico. 151 pp.

Snelling, R. R., G. C. Snelling, J. O. Schmidt, and S. P. Cover. 2009. The sexual castes of *Pogonomyrmex anzensis* Cole (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* 18: 315–321.

Taber, S. 1998. *The World of the Harvester Ants*. Texas A & M Press, College Station, Texas. 213 pp.

J. HYM. RES.
Vol. 18(2), 2009, pp. 326–340

Positive Allometry for Caste Size Dimorphism in *Pheidole* Ants: A New Form of Interspecific Allometry

DONALD H. FEENER JR.

Department of Biology, University of Utah, Salt Lake City, Utah, USA 84112

Abstract.—Alternative phenotypes that differ in body size, shape or other attributes coexist in many animal species, with male-female differences being the most familiar form of alternative phenotypes. Ants are an unappreciated ideal model system to explore allometric interrelationships among alternative phenotypes. Seven different forms of size dimorphism occur within ants, including dimorphisms within and between males and females. In this study I show that a pattern of body size dimorphism parallel to Rensch's rule is found in at least one form of *intra*-sexual dimorphism, that of the sterile worker castes of ants in the genus *Pheidole*. I compared the head and pronotum size of major and minor workers of 105 species of New World *Pheidole* that span the entire range of body size in this genus. Head size of major and minor workers was highly correlated across species ($r = 0.84$, $P < 0.001$), as was pronotum size of the two castes ($r = 0.82$; $P < 0.0001$). Standardized major axis regression of log(head width of major worker) against log(head width of minor worker) showed extreme positive allometry with a slope (β) of 1.53 (95% CI = 1.37–1.71), whereas the analogous regression for pronotal width showed significantly less positive allometry with a slope (β) of 1.22 (95% CI = 1.10–1.37). When adjusted for phylogenetic autocorrelation using phylogenetically independent contrasts, head width allometry was still strongly positive ($\beta = 1.36$, 95% CI = 1.21–1.54), whereas pronotal width allometry was isometric $\beta = 1.09$, 95% CI = 0.94–1.26). I propose several hypotheses to account for positive caste size allometry in ants and suggest that testing them may help point the way to a general class of explanations that encompass both inter- and intrasexual forms of size dimorphism.

Key words.—ants, allometry, caste dimorphism, comparative analysis, phylogenetic analysis, *Pheidole*

Discrete phenotypic classes that differ in adult size, shape or other morphological attributes often coexist within species. These different phenotypic classes may arise from allelic differences among individuals (genetic polymorphisms) or from developmentally induced differences in gene expression in response to different environments experienced by individuals (polyphenisms) (Stern and Emlen 1999; Emlen 2000; Emlen and Nijhout 2000; Evans and Wheeler 2001). Familiar examples of such discrete phenotypic classes include male-female differences in nearly every animal group, alary dimorphism in both male and female insects (Harrison 1980; Roff 1986), size and armament dimorphism in males (Thornhill and Alcock 1983; Fairbairn 1997 and references therein; Emlen and Nijhout 2000), and the sterile and reproductive castes of social insects (Wilson 1971). While these forms of phenotypic dimorphism may have different underlying genetic or developmental origins, all of them presumably evolved, differentiated and persist in species due to the action of natural selection alone or in combination with other evolutionary forces. A major challenge of evolutionary ecology is to identify the evolutionary, developmental and ecological contexts in which these phenotypic classes arise (Emlen and Nijhout 2000; Evans and Wheeler 2001).

The extent of differences among phenotypic classes can vary widely within an evolutionary lineage. For example, quantitative studies of male-female differences in body size, or sexual size dimorphism (SSD), within related groups of organisms often reveal allometric trends in SSD. Abouheif and Fairbairn (1997) have shown that many independent lineages follow a pattern known as "Rensch's rule" (Rensch 1950, 1959): in clades in which females tend to be the larger sex, SSD diminishes in larger species (but see Webb and Freckleton 2007), whereas in clades in which males are the larger sex, SSD increases in larger species. Both these patterns are the result of greater size variation in males relative to females among species in an evolutionary lineage. The underlying causes of these patterns of interspecific allometry are still actively debated (e.g. Blanckenhorn et al. 2007; Webb and Freckleton 2007), but the emerging consensus is that Rensch's rule is the product of differences in selective pressures faced by the two sexes and the underlying genetical or selectional correlations between them (Fairbairn 1997).

Alternative phenotypes also occur *within* one sex in many species. In contrast to SSD, however, patterns of interspecific allometry of intrasexual forms of dimorphism have received little quantitative analysis. These forms of dimorphism, however, offer unexploited opportunities for allometric studies and raise a variety of interesting questions about the evolutionary relationships among alternative phenotypes. Do these intrasexual forms of dimorphism exhibit allometric patterns similar to those described by Rensch's rule? How are allometric patterns of size dimorphism correlated in species with multiple forms of size dimorphism? That is, do the different forms of size dimorphism share the same allometric patterns? How different are the patterns in different evolutionary lineages? What are the underlying microevolutionary processes that give rise to these different macroevolutionary patterns?

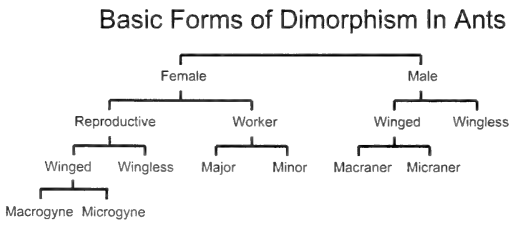


Fig. 1. Basic types of dimorphism in ants. Body size of male and female reproductives is highly variable across species. While females are always larger than males, the difference in size between the sexes is immense in some species and nearly nonexistent in other species. Size differences between female reproductives and female sterile workers are also highly variable among species. In species with dimorphic sterile castes body size of major workers is always larger than body size of minor workers, but species differ in the extent of this size dimorphism. Dimorphism in males is less common in ants than other forms of dimorphism.

Ants are an ideal model system in which to examine interspecific allometric patterns of body size dimorphism and inter-relationships among them. All ants are eusocial with distinct reproductive (male and female) and non-reproductive (sterile female worker) castes (Hölldobler and Wilson 1990). Seven different forms of body size dimorphism exist within ants (Fig. 1). Some of these forms are universal or nearly so, such as the dimorphism between male and female reproductive castes and the dimorphism between reproductive and sterile castes in females (Hölldobler and Wilson 1990; Stubblefield and Seger 1994). Other forms are less ubiquitous, but are nonetheless common enough for comparative analysis. Approximately 15% of all ant genera (45/297) show some degree of size variation or polymorphism in the sterile worker caste (Oster and Wilson 1978). Complete worker dimorphism has evolved independently in at least eight lineages, wherein the two distinct worker subcastes are referred to as major and minor workers. In most species, majors are distinguished from minors by their larger bodies, disproportionately larger heads, and

behavioral specialization (Hölldobler and Wilson 1990). In addition to the plethora of dimorphic forms available in ants, another advantage ants offer allometric studies of body size dimorphism is the great degree of variability in size dimorphism across species. For example, SSD can vary over several orders of magnitude, while mass differences in body size between major and minor workers can vary by up to a factor of 500 (Stubblefield and Seger 1994).

In this paper, I show for the first time that positive interspecific allometry for size dimorphism exists between the sterile worker subcastes of the ant genus *Pheidole*. That is, caste dimorphism is greater in larger species than it is in smaller species. Such an evolutionary pattern of size dimorphism may have a profound effect on how colony labor is divided between worker subcastes in this genus. *Pheidole* (Subfamily Myrmicinae), with over 900 described species, is by far the largest genus with dimorphic worker castes (Bolton 1995; Wilson 2003). In colonies with a normal complement of queens and brood, minor workers perform 30–40 distinct tasks, including those associated with brood and queen care, nest maintenance, foraging and defense (Wilson 1984; Hölldobler and Wilson 1990). Major workers, in contrast, normally perform only 20–70% the number of tasks of minor workers, and appear to be particularly poor at rearing brood (Wilson 1984; Hölldobler and Wilson 1990; Sempo and Detrain 2004). In this genus major workers are apparently specialized for three primary, often mutually exclusive, functions: seed processing, nest site and resource defense, or food storage (Creighton 1966; Wilson 1984; Feener 1987; Hölldobler and Wilson 1990). Behavioral specialization is carried to even greater extremes in some species. For example, major workers of *Pheidole dentata* defend the colony against ants in the genus *Solenopsis*, but they normally do not defend the colony against other ants species (Wilson 1976a, b; Feener 1981) unless they are repeatedly exposed to them (Carlin and Johnston 1984). In the discussion I propose several possible hypotheses that could account for these allometric patterns and suggest further studies of the various forms of body size dimorphism in ants may point the way toward a general class of explanations that encompass all forms of size dimorphism.

In addition to documenting the existence of positive interspecific allometry for caste size dimorphism in the ant genus *Pheidole*, I also evaluate the utility of randomly constructed phylogenies in testing comparative hypotheses (Martins 1996). This technique has been criticized on several grounds (Donoghue and Ackerly 1996; Martins 1996; Abouheif 1998), but may nonetheless be useful in the absence of phylogenetic relationships of focal taxa. Here I show that the use of random phylogenies in the analysis of caste size dimorphism in *Pheidole* compares favorably to the analysis based on the known phylogeny. I conclude that random phylogenies can indeed be useful in comparative studies, despite their limitations.

MATERIALS AND METHODS

I examined interspecific allometry for caste dimorphism in 105 species of *Pheidole* from North and South America (Appendix 1) (Wilson 2003). These species were selected because they were included in the recent phylogenetic analysis of *Pheidole* by Moreau (2008) so that their evolutionary relationships are known. Conveniently, these species also span the entire range of body size found in the genus. For each these species I took the measurements of head width (HW) and pronotal width (PW) for major and minor workers from the descriptions in Wilson (2003). Measurements of each caste are from one individual, often the holotype, paratype or lectotype. Intraspecific variation was ignored in this study. Four of the species included in this study (*obtusospinosa, polymorpha, rhea*

and *tepicana*) possess a supermajor subcaste in addition to major and minor workers (Wilson 2003). This subcaste was not included in analyses.

I estimated interspecific allometry for caste size dimorphism by regressing the log(major worker size) against log(minor worker size) for both head width and pronotal width. I used standardized major axis (SMA) regression to estimate the allometric coefficient (β), or the slope of the regression, and its confidence limits (Model II in Sokal and Rohlf 1995). SMA regression is more appropriate than ordinary least squares regression for data in which both X and Y variables are subject to random error as is the case in most allometric studies (McArdle 1988; LaBarbera 1989; Sokal and Rohlf 1995). SMA regression is also preferable to major axis regression because it is generally more efficient and less biased under a wide range of error variances (McArdle 1988). Calculation of SMA intercept, slope, their confidence intervals (CI) and significance testing followed the recommendations of Warton et al. (2006), using the *R* statistics package *smatr* (Warton et al. 2006).

Regression statistics were calculated for raw, phylogenetically uncorrected data and for phylogenetically independent contrasts (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Martins and Garland 1991; Grafen 1992; Pagel 1992; Purvis et al. 1994) as calculated from the phylogenetic relationships of the 105 species included in the study. I used the "pic" command in the *R* statistics *ape* package to calculate 104 phylogenetically independent contrasts (Paradis 2006). Regressions for the phylogenetically independent contrasts were forced through the origin as recommended by Garland et al. (1992). There was no evidence of nonlinearities in these relationships which would invalidate this procedure (Quader et al. 2004).

To further analyze how caste dimorphism changes with body size, I calculated a caste dimorphism index (CDI) that is analogous to the sexual dimorphism index (SDI) of Lovich and Gibbons (1992). I defined CDI = log(major worker size) − log(minor worker size).

In the absence of a known phylogeny, Martins (1996) recommended using "random" phylogenies to account for phylogenetic autocorrelation. Despite its limitations (Donoghue and Ackerly 1996; Martins 1996; Abouheif 1998), this procedure is potentially very useful in testing comparative hypotheses in lineages for which phylogenetic relationships are not yet known. To see how useful Martins's procedure would be in the present study, I compared the results of randomly generated phylogenies against the results of the known phylogeny by generating two random sets of 1000 phylogenetic trees, one assuming a "standard" time only model of speciation and the other assuming a "coalescent" model of speciation (see Martins 1996 for differences between these models). For each random tree I then generated 104 independent contrasts in head width and pronotal width for major and minor workers. I then performed SMA regression analyses on these independent contrasts to estimate the allometric coefficient (β) and its confidence limits (CIs). These regressions were forced through the origin as they were for the known phylogeny (Garland et al. 1992). Confidence intervals (CI) of the mean β for 1000 trees were estimated by ordering the slope values and taking the lowest 2.5% value as the low confidence limit and taking the highest 2.5% value as the high confidence limit. Randomized trees were generated using the "rtree" and "rcoal" commands in the *R* statistics *ape* package, for standard and coalescent models of speciation, respectively (Paradis 2006). Phylogenetically independent contrasts and regression analysis were calculated as above for the known phylogeny.

RESULTS

Analysis of Phylogenetically Uncorrected Data

Head width of major workers was 5.4 times more variable than head width of minor workers across the 105 species included in this study (coefficients of variation for log-transformed data were 1.79 for major workers vs. 0.33 for minor workers). Despite the difference in size variation, head width of major workers was nevertheless strongly correlated with head width of minor workers ($r = 0.84$, $P < 0.001$; Fig. 2A). Phylogenetically uncorrected interspecific allometry for caste size dimorphism in head width showed strong positive allometry (Table 1; Fig. 2A). The allometric slope of the SMA regression ($\beta = 1.53$, 95% CI = 1.37–1.71) was significantly greater than 1.00 ($P < 0.001$). Such positive allometry means that larger species are more caste dimorphic than smaller species, as indicated by the significant positive correlation ($r = 0.26$, $P = 0.007$) between the caste dimorphism index (CDI) and log(head width of minor workers) (Fig. 2B).

Pronotal width of major workers was only 2.4 times more variable than pronotal width in minor workers (coefficients of variation for log-transformed data were 0.53 for major workers vs. 0.22 for minor workers). The correlation among subcastes for pronotal width was similar to that found for head width ($r = 0.82$, $P < 0.0001$; Fig. 2C). As with head width, phylogenetically uncorrected interspecific allometry for caste size dimorphism in pronotal width was strongly positive (Table 1; Fig. 2C). The allometric slope of the SMA regression ($\beta = 1.22$; 95% CI = 1.10–1.37) was significantly greater than 1.00 ($P < 0.0007$), but the CDI showed no significant correlation with log(pronotal width of minor workers) ($r = 0.03$, $P = 0.7$; Fig. 2D). Although the slopes for both head width and pronotal width allometry were significantly greater than 1.00, the slope for pronotal width was significantly less than that for head width ($P = 0.0002$). This means that across species, head width dimorphism increases more steeply with size than pronotal width.

Analysis of Phylogenetically Independent Contrasts

Results of regression analyses of the independent contrasts derived from Moreau's phylogenetic tree qualitatively supported the results derived from the non-phylogenetic analyses (Table 1 and Fig. 3). Independent contrasts of head width of major and minor workers were strongly correlated with one another ($r = 0.78$, $P < 0.001$; Fig. 3A) and showed strong positive allometry (Table 1; Fig. 3A). The allometric slope of the SMA regression ($\beta = 1.36$, 95% CI = 1.21–1.54) was less than that for the phylogenetically uncorrected data, but it was still significantly greater than 1.00 ($P < 0.001$). Independent contrasts of pronotal width of major and minor workers were also strongly correlated with one another ($r = 0.66$, $P < 0.001$; Fig. 3B), but their relationship was now isometric rather than positively allometric as it was for the phylogenetically uncorrected data (Table 1; Fig. 3B). The allometric slope of the SMA regression ($\beta = 1.09$, 95% CI = 0.94–1.26), did not differ significantly from 1.00. Just as seen in the phylogenetically uncorrected data, the slope for pronotal width was significantly less than that for head width ($P = 0.003$), reinforcing the conclusion that across species, head width dimorphism increases more steeply with size than pronotal width dimorphism.

Analysis within castes of the interspecific allometry for head width versus pronotal width revealed two underlying patterns that contributed to the positive allometry for caste dimorphism described above (Fig. 4). First, allometry for log(head width) on log(pronotal width) in major workers was weakly positive or isometric ($\beta = 1.11$, 95% CI = 1.04–1.19 for raw data;

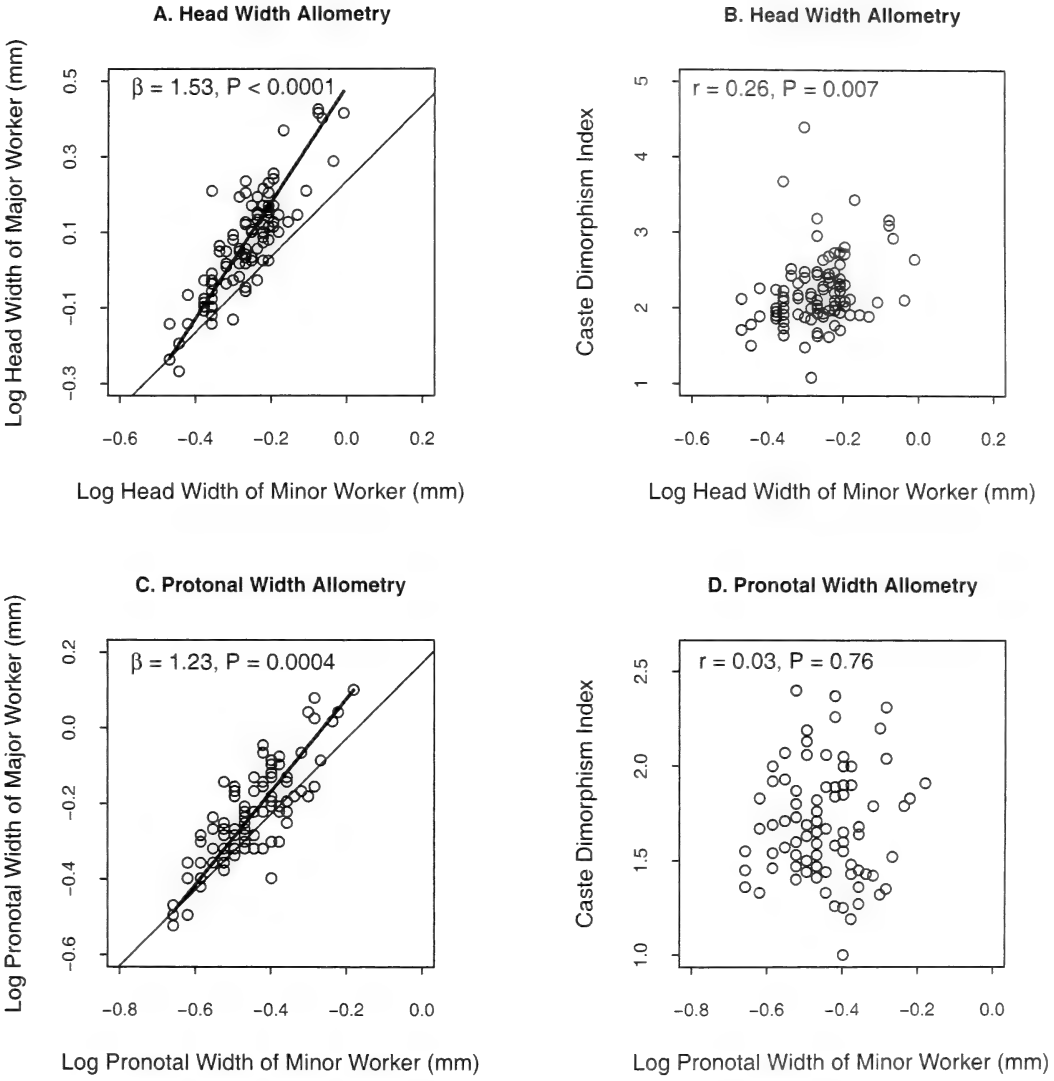


Fig. 2. Phylogenetically uncorrected allometric relationships between major and minor worker castes in New World members of the ant genus *Pheidole* (n = 105 species). Heavy solid line is SMA regression line, light solid line is isometry reference line of $\beta = 1$. A. Interspecific allometry for caste size dimorphism using head width as a measure of body size. Equation for the SMA regression is: log(head width of major worker) = −0.58 + 1.53[log(head width of minor worker)], $r = 0.84$. Slope of the line is significantly greater than 1.00 ($P < 0.0001$). B. Correlation between the index of caste dimorphism and log(head width of minor workers), $r = 0.26$, $P < 0.007$. C. Interspecific allometry for caste size dimorphism using pronotal width as a measure of body size. Equation for the SMA regression is log(pronotal width of major worker) = −0.34 + 1.23[log(pronotal width of minor worker)], $r = 0.82$. Slope of the line is significantly greater than 1.00 ($P = 0.0004$). D. Correlation between the caste dimorphism index and log(pronotal width of minor workers), $r = 0.03$, $P = 0.76$.

β = 1.09, 95% CI = 0.99–1.21 for phylogenetically independent contrasts), which means that relative to pronotal width major workers have slightly disproportionately or proportionately *larger* heads in larger species. Second, this same allometry in minor workers was strongly negative (β = 0.89, 95% CI = 0.83–0.95 for raw data; β = 0.87, 95% CI = 0.79–0.97 for phylogenetically independent contrasts), which

Table 1. Summary statistics for the slope of SMA regressions of A. log(head width of major worker) on log(head width of minor worker) and B. log(pronotal width of major worker) on log(pronotal width of minor worker). Uncorrected data were not adjusted for phylogenetic "non-independence." Independent contrasts were adjusted for phylogenetic "non-independent". Random independent contrasts were based on 1000 randomly generated phylogenies that assumed either a standard speciation model or a coalescent speciation model (see Martins 1996, 1999 and Paradis 2006 for details). Var_P is the variance resulting from uncertainity in the phylogeny and Var_S is the variance resulting from deviations of the species data points from the predicted model (Martins 1996).

			Random independent contrasts	
Statistic	Uncorrected data	Independent contrasts	Standard model	Coalescent model
A. Regression for head width of major workers on head width of minor workers				
Correlation coefficient	0.84	0.78	0.83	0.81
Slope estimate	1.53	1.36	1.50	1.55
Var_P	0.0000	0.0000	0.0098	0.7593
Var_S	0.0069	0.0068	0.0069	0.0144
Total se	0.0830	0.0826	0.1295	0.8796
95% confidence interval	$1.37 < \beta < 1.71$	$1.21 < \beta < 1.54$	$1.32 < \beta < 1.69$	$0.94 < \beta < 2.32$
B. Regression for pronotal width of major workers on pronotal width of minor workers				
Correlation coefficient	0.82	0.66	0.84	0.84
Slope estimate	1.23	1.09	1.27	1.31
Var_P	0.0000	0.0000	0.0067	0.1476
Var_S	0.0048	0.0066	0.0046	0.0057
Total se	0.0690	0.0810	0.1062	0.3915
95% confidence interval	$1.10 < \beta < 1.37$	$0.94 < \beta < 1.26$	$1.13 < \beta < 1.43$	$0.81 < \beta < 2.07$

means that relative to pronotal width minor workers have disproportionately *smaller* heads in larger species. Any hypothesis advanced to explain positive allometry for caste dimorphism should account for both the slight positive allometry or isometry in relative head size of major workers, and the strong negative allometry in relative head size in minor workers.

Random Phylogenies

Correlation coefficients and slope estimates from the randomly generated phylogenies were nearly identical to the phylogenetically uncorrected values (Table 1). The underlying speciation model used to construct the phylogenetic trees had little effect on mean slope estimates or correlation coefficients, but the coalescent model produced substantially wider variance in the distribution of slope values and therefore wider 95% CIs than did the standard model (Table 1 and Fig. 5). The total standard error of the slope estimates for the random phylogenies were substantially larger (1.3–10.6 times) than the estimates for the uncorrected data or the independent contrasts. This increase was due entirely to the added variance associated with phylogenetic uncertainty (Var_P in Table 1). In fact, variance attributed to deviation of the species data points from the regression model (Var_S) was nearly the same for all analyses.

The distributions of slope estimates from the randomly constructed trees were extremely leptokurtic around the mean values of the uncorrected data (Fig. 5). The leptokurtic nature of these distributions kept the empirically derived 95% CIs smaller than they would have been if estimated from normal theory. For head width allometry all the models predicted the same qualitative pattern of significantly positive allometry for head width of major workers plotted against the head width of minor workers. In contrast, the qualitative pattern of pronotal width allometry was isometric in the independent contrasts and the random phylogenies based on the coalescent model, and significantly posi-

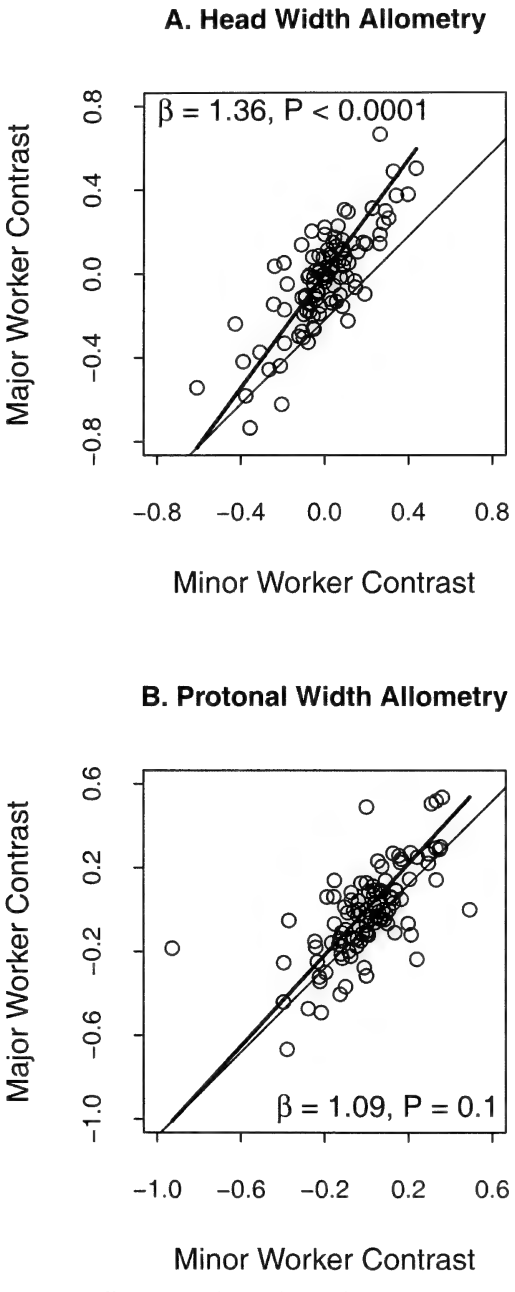


Fig. 3. Allometric relationships of phylogenetically independent contrasts between major and minor worker castes in New World members of the ant genus *Pheidole* (n = 104 contrasts). Heavy solid line is SMA regression line, light solid line is isometry reference line of β = 1. A. Interspecific allometry for caste size dimorphism using head width as a measure of body size. Equation for the SMA regression is: major worker contrast = 0.00 + 1.36(minor worker contrast), r = 0.79. Slope of the line is significantly greater than 1.00 (P < 0.0001). B. Interspecific allometry for caste size dimorphism using pronotal width as a measure of body size. Equation for the SMA regression is major worker contrast = 0.00 + 1.08(minor worker contrast), r = 0.66. Slope of the line is not significantly different from 1.00 (P = 0.1).

tive in the uncorrected data and in the random phylogenies based on the standard model.

DISCUSSION

Results of this study uncovered three patterns of variation that must be explained in building an understanding of positive allometry for caste size dimorphism in *Pheidole*. First, head size of major workers is more variable among species than head size of minor workers. The greater size variability in major workers yields an allometric coefficient greater than 1.00 when head size of major workers is plotted against head size of minor workers (Fig. 2). Second, despite the greater interspecific variability in head size among major workers, head size of major and minor workers are highly correlated with one another across species (Table 1). Third, allometry for head size against pronotal width in major workers is isometric or weakly positive, whereas allometry for head size against pronotal width in minor workers is strongly negative (Fig. 4).

Evolutionary Processes Underlying Positive Allometry for Caste Size Dimorphism

An understanding of positive allometry for caste size dimorphism in ants requires that we account for both the greater variance in size of major workers than minor workers *and* the high correlation in size between castes. Here I argue that diversifying directional selection on colonies has led to the greater size variance in the major worker caste and that the high correlation in size between castes is a product of either a correlated response to selection in the minor worker caste due to

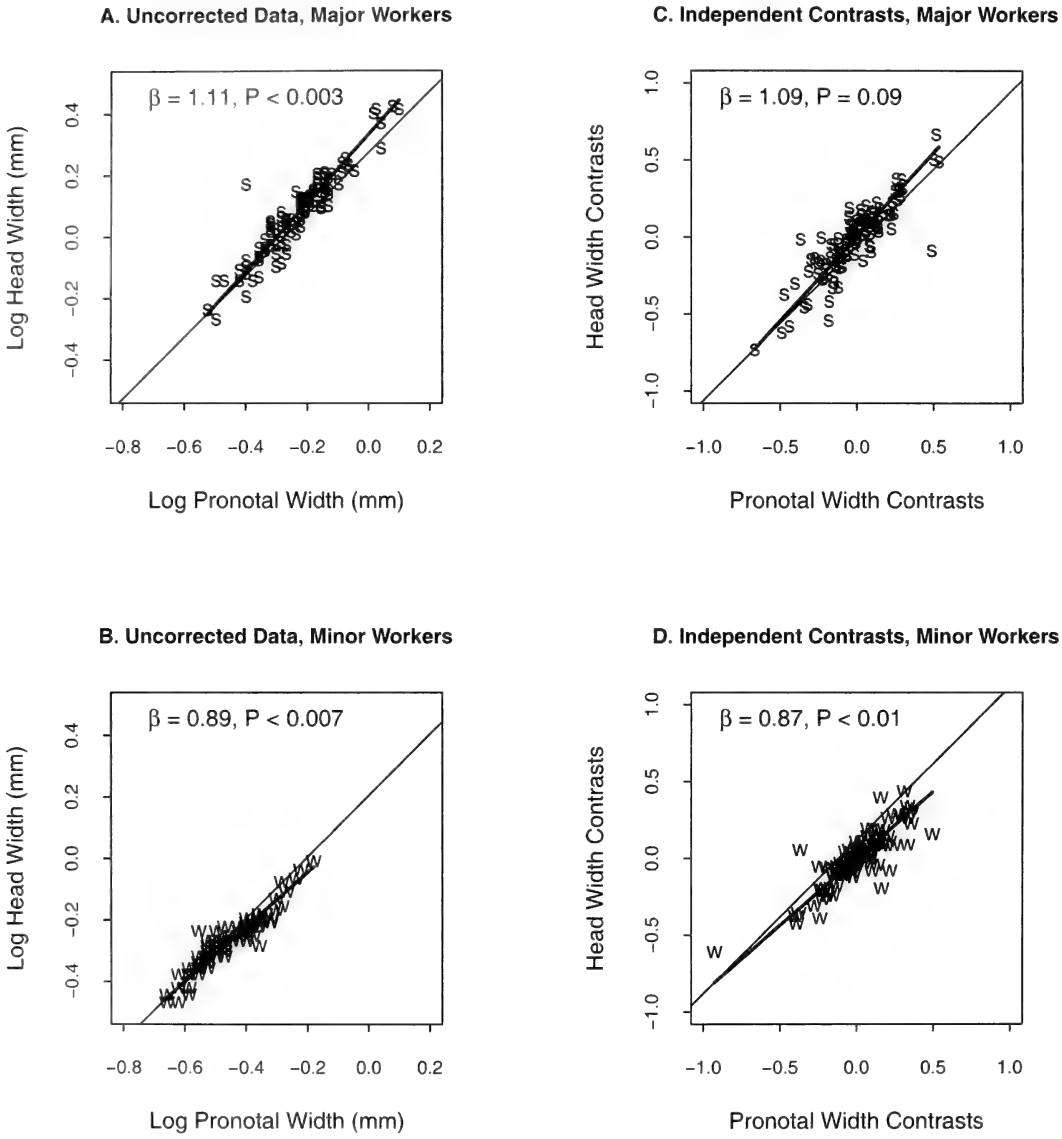


Fig. 4. Allometric relationships of head size versus pronotum size in major and minor workers in New World members of the genus *Pheidole* (n = 105 in A. and B., n = 104 in C. and D.). Heavy solid line is SMA regression line, light solid line is isometry reference line of β = 1. A. Interspecific allometry of head width versus pronotal width in major workers for raw, uncorrected data. Equation for the SMA regression is: log(head width of major worker) = 0.33 + 1.11[log(pronotal width of major worker)], r = 0.93. Slope of the line is significantly greater than 1.00 ($P < 0.003$). B. Interspecific allometry of head width versus pronotal width in minor workers for raw, uncorrected data. Equation for the SMA regression is: log(head width of minor worker) = 0.13 + 0.89[log(pronotal width of minor worker)], r = 0.94. Slope of the line is significantly less than 1.00 ($P < 0.007$). C. Interspecific allometry of head width versus pronotal width in major workers for phylogenetically independent contrasts for major workers. Equation for the SMA regression is: log(head width contrast) = 0.00 + 1.09[log(pronotal width contrast)], r = 0.86. Slope of the line is significantly greater than 1.00 ($P < 0.003$). D. Interspecific allometry of head width versus pronotal width in major workers for phylogenetically independent contrasts for minor workers. Equation for the SMA regression is: log(head width contrast) = 0.00 + 1.09[log(pronotal width contrast)], r = 0.84. Slope of the line is significantly less than 0.87 ($P < 0.01$).

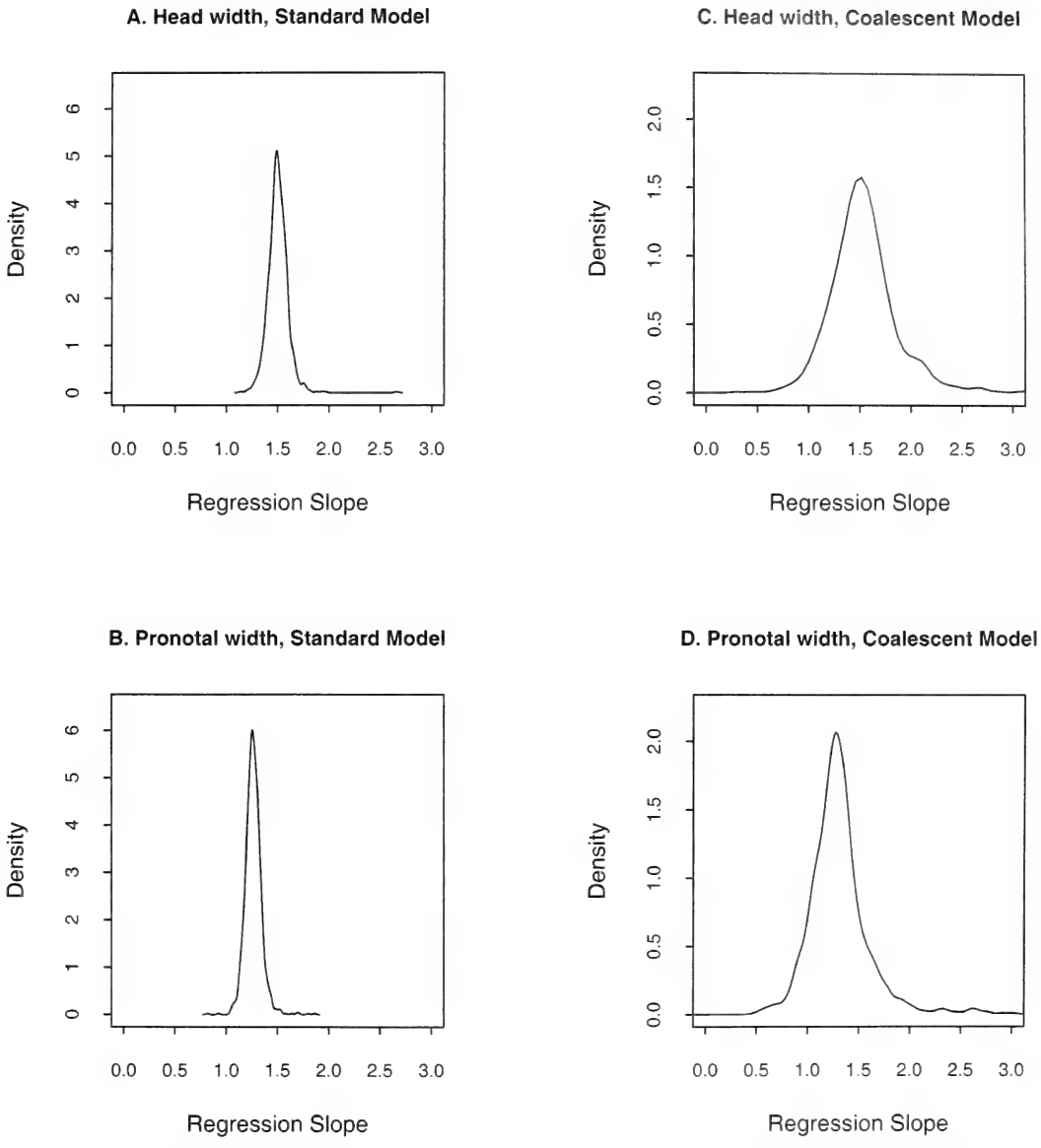


Fig. 5. Distributions of regression slopes derived from 1000 randomly constructed phylogenies. Slope estimate for each phylogeny was based on 104 independent contrasts of 105 species. $g_2 \pm$ sek is the kutosis coefficient and its standard error ($24/n$). A distribution is considered significantly leptokurtic if $g_2/\text{sek} > 2.00$. A. Regression slopes for log(head width of major workers) on log(head width of minor workers). Phylogenies assumed standard speciation model. $g_2 = 22.38 \pm 0.15$, $P < 0.05$. B. Regression slopes for log(pronotal width of major workers) on log(pronotal width of minor workers). Phylogenies assumed standard speciation model. $g_2 = 10.29 \pm 0.15$, $P < 0.05$. C. Regression slopes for log(head width of major workers) on log(head width of minor workers). Phylogenies assumed coalescent speciation model. $g_2 = 612.88 \pm 0.15$, $P < 0.05$. D. Regression slopes for log(pronotal width of major workers) on log(pronotal width of minor workers). Phylogenies assumed coalescent speciation model. $g_2 = 42.65 \pm 0.15$, $P < 0.05$.

high genetic correlations between castes (Lande 1980) or colony-level correlational selection affecting minor workers as a result division of labor between castes (Zeng 1988).

Major workers in many species of *Pheidole* are specialized to defend their colony's nest site and/or food sources against other colonies of ants (Hölldobler and Wilson 1990). The hypertrophic head of this caste houses large, powerful muscles used to work the mandibles, the most effective weapon major workers have against enemy ants. Within species there may be strong, directional colony-level selection to increase fighting effectiveness of major workers by enlarging the head and thereby enhancing the strength of the mandibles. This hypothesis requires that directional selection intensity on major workers is greater than on minor workers, at least for the behaviors for which majors are specialized. This pattern is likely to be true in general because defense by major workers is often critical to colony survival and reproduction. A similar argument may hold for species in which the major workers are specialized for seed processing. Selection for increased head size and stronger mandibles in major workers of seed harvesting species probably allows access to a greater range of seed size and/or seed coat hardness. In contrast, head size of minor workers may be under strong stabilizing selection as suggested by the strong interspecific negative allometry of head width relative to pronotal width seen in this caste (Fig. 4). A relatively constant head size may be selected as a result of the general nature of the tasks performed by minor workers or their primary role in care of small eggs and larvae (Hölldobler and Wilson 1990). These caste-specific differences in selection pressure may be sufficient to account for the positive allometry in CSD, but they cannot account for the high correlation in size between castes.

As selection acts to increase head size of major workers, head size of minor workers may also increase through a correlated response to selection due to a high genetic correlation between major and minor workers (Lande 1980, Fairbairn and Preziosi 1994, Fairbairn 1997). Because these castes share a common developmental pathway until late in the last larval instar (Wheeler 1991), genetic correlations between major and minor workers should be as high as or higher than those observed between the sexes (typically > 0.80 for body size, see Lande 1980, Fairbairn 1997). Existence of high genetic correlations between major and minor workers may bias the direction of morphological divergence among species along "genetic lines of least resistance," thus maintaining the phenotypic correlation between castes for long periods of time, even in the face of strong natural selection (Schluter 1996).

An alternative hypothesis for the high correlation between size of major and minor workers is the presence of correlational selection due to the behavioral interactions between worker castes. Proper coordination of division of labor within the colony requires that major and minor workers routinely interact with one another (Hölldobler and Wilson 1990). For example, major and minor workers often exchange food and information with one another through trophallaxis and antennal contact (Hölldobler and Wilson 1990). These necessary interactions make it likely that the efficiency at which each caste performs its duties is not independent of the other caste. Workers that differ too much in size might not be capable of efficient interactions and colony functioning as a whole would therefore suffer. Hence, one might expect that, as head size of major workers increases in response to the defense or seed processing needs of the colony, minor workers would experience correlational selection for increased head size as a result of pressures for efficient interactions among caste members. This hypothesis has the advantage that a high

correlation in size between castes is not only possible at an evolutionary equilibrium, it is expected as an integral part of colony-level efficiency.

Testing the validity of these hypotheses is a major challenge for future work. It will require measurement of genetic correlations between major and minor workers, assessment of caste differences in the intensity of selection under reasonably natural conditions, and a comparison of selection pressures across species that vary in size. A primary goal of this future work should be an explanation of the increasing divergence between castes with an increase in body size.

Comparative Analysis in the Absence of a Phylogeny

The newly available phylogeny for over 100 species of *Pheidole* (Moreau 2008) provided a unique opportunity to assess the use of randomly constructed phylogenies (Martins 1996) in studies of interspecific allometry. In the present study, analysis of head width allometry using phylogenetically uncorrected data and random phylogenies gave the same qualitative results as an analysis using phylogenetically independent contrasts (Table 1). Similar analyses for pronotal width allometry found that phylogenetically uncorrected data and random phylogenies based on a standard speciation model gave different qualitative results from an analysis using phylogenetically independent contrasts. Results from random phylogenies based on a coalescent model of speciation, however, gave qualitatively similar results to phylogenetically independent contrasts, due to the larger 95% CIs of the coalescent model. While the use of random phylogenies in comparative analysis has several weaknesses (Donoghue and Ackerly 1996; Martins 1996;Abouheif 1998), this study illustrates how cautious application of this approach can be used to test novel comparative hypotheses in lineages lacking phylogenetic information.

Conclusions

Ants offer unexploited opportunities for comparative studies of body size dimorphism and morphological integration (Pie and Traniello 2006). All free-living species of ants exhibit at least two forms of body size dimorphism: differences between males and reproductive females and differences between reproductive females and sterile worker females. In some species there also may be body size differences in major and minor castes of sterile workers or between winged and wingless males. How these different forms of body size dimorphism are inter-related within and among species has only recently begun (Pie and Traniello 2006). This study demonstrates for the first time that an allometric pattern parallel to Rensch's rule in sexual dimorphic species also holds for the sterile worker castes of ants in the genus *Pheidole*. Results of this study suggest that a size-related gradient in the intensity of sexual selection cannot be the only underlying process that explains the pattern of increasing dimorphism with increasing body size. Instead, sexual selection may be simply one form of a general class of selection processes in which intensity varies with changes in body size. A goal of future research should be the characterization of these selection processes and identification of ones that give rise to patterns parallel to Rensch's rule. Besides the sterile worker castes of ants, other forms of intrasexual dimorphism occur in a wide variety of insect groups. These groups offer numerous opportunities for exploring evolutionary divergence in body size and assessing the universality of the underlying mechanisms responsible for it.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Roy R. Snelling, a friend, mentor and endearing curmudgeon. I am deeply grateful for the kindness and advice he gave me on my visits to the LACM over the years. I will miss sharing Mexican food and Negras Modelos with him. I thank Corrie Moreau for generously

providing the NEXUS file of her phylogeny of *Pheidole* before it was published. I also thank D. E. Wheeler for many discussions on worker caste polymorphism over the years, E. P. Martins for advice on random phylogenies and M. R. Pie for comments on a previous version of this manuscript. I also thank two anonymous reviewers for comments on the manuscript. Support of NSF grant DEB03-16524 is gratefully acknowledged.

LITERATURE CITED

Abouheif, E. 1998. Random trees and the comparative method: a cautionary tale. *Evolution* 52: 1197–1204.

——— and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149: 540–562.

Blanckenhorn, W. U., A. F. G. Dixon, D. J. Fairbairn, M. W. Foellmer, P. Gibert, K. van der Linde, R. Meier, S. Nylin, S. Pitnick, C. Schoff, M. Signorelli, T. Teder, and C. Wiklund. 2007. Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* 169: 247–257.

Bolton, B. 1995. *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, MA.

Carlin, N. F. and A. B. Johnston. 1984. Learned enemy specification in the defense recruitment system of an ant. *Naturwissenschaften* 71: 156–157.

Creighton, W. S. 1966. The habits of *Pheidole ridicula* Wheeler with remarks on habit patterns in the genus *Pheidole* (Hymenoptera: Formicidae). *Psyche* 73: 1–7.

Donoghue, M. J. and D. D. Ackerly. 1996. Phylogenetic uncertainties and sensitivity analyses in comparative biology. *Philosophical Transactions of the Royal Society of London, Series B* 351: 1241–1249.

Emlen, D. J. 2000. Integrating development with evolution: a case study with beetle horns. *Bioscience* 5: 403–418.

——— and H. F. Nijhout. 2000. The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology* 45: 661–708.

Evans, J. D. and D. W. Wheeler. 2001. Gene expression and the evolution of insect polyphenisms. *BioEssays* 23: 1–7.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28: 659–687.

——— and R. F. Preziosi. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. *American Naturalist* 144: 101–118.

Feener, D. H., Jr. 1981. Competition between ant species: outcome controlled by parasitic flies. *Science (Washington, D.C.)* 214: 815–817.

———. 1987. Response of *Pheidole morrisi* to two species of enemy ants, and a general model of defense behavior in *Pheidole* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 60: 569–575.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using plylogenetically independent contrasts. *Systematic Biology* 41: 18–32.

Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B* 326: 119–157.

———. 1992. The uniqueness of the phylogenetic regression. *Journal of Theoretical Biology* 156: 405–423.

Harrison, R. G. 1980. Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics* 11: 95–118.

Harvey, P. H. and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.

Hölldobler, B. and E. O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, MA.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20: 97–117.

Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* 34: 292–307.

Lovich, J. E. and J. W. Gibbons. 1992. A review of techniques for quantifying sexual dimorphism. *Growth, Development and Aging* 56: 269–281.

Martins, E. P. 1996. Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* 50: 12–22.

——— and T. Garland. 1991. Phylogenetic analysis of the correlated evolution of continuous characters: a simulation study. *Evolution* 45: 534–557.

McArdle, B. H. 1988. The structural relationship: regression in biology. *Canadian Journal of Zoology* 66: 2329–2339.

Moreau, C. S. 2008. Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 48: 224–239.

Oster, G. F. and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, NJ.

Pagel, M. D. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* 156: 431–442.

Paradis, E. 2006. *Analysis of phylogenetics and evolution with R*. Springer, New York, NY.

Pie, M. R. and J. F. A. Traniello. 2006. Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. *Journal of Zoology* 271: 99–109.

Purvis, A., J. L. Gittleman, and H. K. Luh. 1994. Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *Journal of Theoretical Biology* 167: 293–300.

Quader, S., K. Isvaran, R. E. Hale, B. G. Miner, and N. E. Seavy. 2004. Nonlinear relationships and phylogenetically independent contrasts. *Journal of Evolutionary Biology* 17: 709–715.

Rensch, B. 1950. Die Abhangigkeit der relativen sexualdifferenz von der Kopergroße. *Bonner Zoologische Beiträge* 1: 58–69.

———. 1959. *Evolution above the species level.* Columbia University Press, New York, NY.

Roff, D. A. 1986. The evolution of wing dimorphism in insects. *Evolution* 40: 1009–1021.

Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50: 1766–1774.

Sempo, G. and C. Detrain. 2004. Between-species differences of behavioural repertoire of castes in Pheidole ant genus: methodological artefact? *Insectes Sociaux* 51: 48–54.

Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research.* 3rd edition. W. H. Freeman and Company, San Francisco, CA.

Stern, D. L. and D. J. Emlen. 1999. The developmental basis for allometry in insects. *Development* 126: 1091–1101.

Stubblefield, J. W. and J. Seger. 1994. Sexual dimorphism in the Hymenoptera. Pp. 71–103 *in* R. V. Short, and E. Balaban eds. *The differences between the sexes.* Cambridge University Press, Cambridge, UK.

Thornhill, R. and J. Alcock. 1983. *The evolution of insect mating systems.* Harvard University Press, Cambridge, MA.

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biological Review* 81: 259–291.

Webb, T. J. and R. P. Freckleton. 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch's rule. *PLoS ONE* 2: e897.

Wheeler, D. E. 1991. The developmental basis of worker caste polymorphism in ants. *American Naturalist* 138: 1218–1238.

Wilson, E. O. 1971. *The insect societies.* The Belknap Press of Harvard University Press, Cambridge, MA.

———. 1976a. Behavioral discretization and the number of castes in an ant species. *Behavioral Ecology and Sociobiology* 1: 141–154.

———. 1976b. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 1: 63–81.

———. 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 16: 89–98.

———. 2003. *Pheidole in the New World: a dominant, hyperdiverse ant genus.* Harvard University Press, Cambridge, MA.

Zeng, Z.-B. 1988. Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* 42: 363–374.

APPENDIX 1. List of *Pheidole* species included in the study. Species with a trimorphic worker caste are indicated in bold type.

absurda	*crassicornis*	*macrops*	*sciophila*
adrianoi	*davisi*	*mamore*	*scrobifera*
allarmata	*dentata*	*megacephala*	*senex*
amazonica	*desertorum*	*metallescens*	*sensitiva*
artemisia	*diana*	*micula*	*sicaria*
astur	*diversipilosa*	*militicida*	*sitiens*
barbata	*dossena*	*minutula*	*soritis*
bicarinata	*erratilis*	*moerens*	*sospes*
biconstricta	*fimbriata*	*morrisi*	*spadonia*
boltoni	*fiorii*	*nitella*	*striaticeps*
boruca	*fissiceps*	*nitidicollis*	*subarmata*
browni	*flavens*	*obscurithorax*	***tepicana***
californica	*floridana*	***obtusospinosa***	*titanis*
caltrop	*furtiva*	*pacifica*	*tristicula*
carrolli	*gilvescens*	*pelor*	*truncula*
casta	*granulata*	*perpilosa*	*tucsonica*
cavigenis	*harlequina*	*pilifera*	*tysoni*
cephalica	*hoplitica*	***polymorpha***	*umphreyi*
cerebrosior	*hyatti*	*portalensis*	*vallicola*
ceres	*indagatrix*	*prostrata*	*vinelandica*
clementensis	*indistincta*	*psammophila*	*violacea*
clydei	*innupta*	***rhea***	*vistana*
cocciphaga	*jelskii*	*rhinoceros*	*xerophila*
cockerelli	*juniperae*	*rufescens*	*yaqui*
coloradensis	*laselva*	*rugulosa*	
constipata	*laticornis*	*sagittaria*	
cramptoni	*littoralis*	*sciara*	

J. HYM. RES.
Vol. 18(2), 2009, pp. 341–360

An Experimental Study of Microbial Nest Associates of Borneo's Exploding Ants (*Camponotus* [*Colobopsis*] species)

D. W. DAVIDSON*, N. F. ANDERSON, S. C. COOK**, C. R. BERNAU†, T. H. JONES, A. S. KAMARIAH, L. B. LIM, C. M. CHAN AND D. A. CLARK‡

(DWD, NFA, SCC, CRB) Department of Biology, University of Utah, Salt Lake City, Utah, USA
(THJ, DAC) Virginia Military Institute, Department of Chemistry, Lexington, VA, USA
(ASK) Department of Biology, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam
(LBL, CMC) Department of Chemistry, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam

Abstract.—Cavity nesting ants in the *Camponotus* (*Colobopsis*) *cylindricus* (COCY) complex possess hugely hypertrophied mandibular gland (MG) reservoirs containing weakly acidic phenolic acetogenins and/or diterpenes unique for insects. Many taxa ("exploding ants") use these products in suicidal defense of territory, but major workers of all species, and all workers of some species, possess hypertrophied reservoirs and clade-typical products not used in suicidal fights. An additional role of MG products in nest hygiene was suspected. We sampled microbial associates of nest cavity fiber and carton shelving in artificial wooden nests occupied by substantial colony fragments of COCY species and compared them with two controls: microbes in unoccupied nests and nests occupied by other cavity-nesting ant species. Several natural nests in fallen wood were also sampled. Bacteria and fungi cultured on malt extract agar were identified from gene sequences amplified by universal bacterial and fungal primers. Results were related to an expanded data base on MG chemistry. Twenty-four of 55 nests were colonized by ants, mostly by COCY species, nesting naturally or not in dead wood. In colony-level analyses, mycoparasitic *Trichoderma* fungi were significantly over-represented in nest fiber of COCY species. Their detection was restricted to taxa naturally inhabiting fallen wood; the majority of these taxa produced *m*-cresol as the major component of MG volatiles. *Burkholderia* bacteria were significantly more common in COCY species' nests than in unoccupied nests but only when replicate nests per colony were allowed. *Trichoderma* and *Burkholderia* tended to co-occur in nest fiber, perhaps due to traits influencing arrival and survival. Both *Trichoderma* and *Burkholderia* may contribute to nest hygiene, and their joint occurrence could potentially affect longevity of nests in dead wood. Both genera also occur as endophytes, and interactions between ants and endophytes merit further study. Documented over-representation in live hosts of genera *Antidesma* and *Cleistanthus* [Phyllanthaceae]) could be related to the microbial environment provided by these hosts.

"From the information available, ants universally reject fungi ... as inquilines in their living quarters, although this generalization merits further investigation" (Sánchez-Peña 2005)

Eusociality has long been recognized as a life style conveying high vulnerability to pathogens (e.g. Hamilton 1972; Shykoff and Schmid-Hempel 1991). Extranidal activities regularly expose foragers to diverse microbes, including potential pathogens that may spread rapidly among numerous closely interacting and genetically similar individuals at the nest. Such threats are evident from the ants' early evolution of metapleural glands, located on the posterolateral mesosoma and functioning in

* Author for correspondence
** Department of Entomology, Texas A & M University, College Station, TX, USA
† College of Natural Resources, University of Idaho, Moscow, ID, USA
‡ Max-Planck-Institut für Kohlenforschung, Mülheim, Germany

antisepsis (e.g. Maschwitz et al. 1970; Maschwitz 1974; Macintosh et al. 1995; Bot et al. 2002; reviewed in Hölldobler and Wilson 1990). Unique to the ants, these exocrine glands produce mainly proteinaceous compounds (do Nascimento et al. 1996), augmented in at least some taxa by volatile organic components (do Nascimento et al. 1996; Ortius-Lechner et al. 2000; Jones et al. 2005).

Adaptations against detrimental nest microbes are best studied in leaf-cutter ants (tribe Attini), where diverse ant traits oppose both potential pathogens and a dangerous parasite of the fungal garden that sustains developing larvae (reviewed in Currie and Stewart 2001; Bot et al. 2001a; Hughes et al. 2002; Mueller et al. 2005; Fernández-Marín et al. 2006; Little et al. 2006; Zhang et al. 2007). Various metapleural gland volatiles are differentially effective against different categories and life history stages of microorganisms, and this diversity of compounds may guard against the evolution of resistance in pests (Bot et al. 2002). Complementing these secretions are specific, evolved behaviors including grooming, weeding, and waste management (reviewed in Bot et al. 2001a; Currie and Stewart 2001; Hart and Ratnieks 2001; Mueller et al. 2005; Fernández-Marín et al. 2006; Little et al. 2006; Zhang et al. 2007). Additionally, to oppose a dangerous parasite of the fungal garden (a fungus resistant to metapleural gland volatiles; Bot et al. 2002), workers maintain an antibiotic-producing natural enemy of the parasite (Currie et al. 1999a; Currie 2001; Gerardo et al. 2006; Little and Currie 2007, 2008). The beneficial actinomycete bacteria can potentially evolve rapidly to combat a constantly evolving pest (Currie et al. 1999b, 2003a,b; Currie 2001; Mueller et al. 2005; Poulsen et al. 2005; Little et al. 2006; but see Gerardo and Caldera 2007). Given the advantage of this strategy, it would be surprising if other ant taxa had not evolved to use beneficial microbes as antagonists to microbial enemies.

Despite near ubiquity of metapleural glands in the worker caste of ants, many members of the highly species-rich and cosmopolitan tribe Camponotini have lost the glands secondarily (Hölldobler and Engel-Siegel 1984). How might nest hygiene be maintained in these taxa? Possibilities include restriction of nests to less pathogen-plagued substrates, frequent movement of colonies to new nests, and/or transfer of antiseptic function to other glands (Maschwitz et al. 1970; Cole 1975). Alternatively, or in addition, these ants might exploit antiseptic properties of beneficial microbes. Further, because costs of anti-pathogen defense can be significant (e.g. Poulsen et al. 2002, 2003; Currie et al. 2003b), defensive costs might be reduced by basing defense mechanisms on nutrients present in abundance or excess. For example, in frequently nitrogen-limited camponotines (Davidson 2005), costs might be reduced by deploying defenses based on investments of carbon, rather than nitrogen, i.e., on volatile organics, rather than proteins.

To better understand resistance to nest pathogens in taxa lacking metapleural glands, we focused on a well-resolved 15-member clade of cavity-nesting camponotines in which variation in nesting habits likely correlates with differential exposure to nest pathogens (Cook 2008). Coexisting locally in a Bornean rain forest, species in the *Camponotus* (*Colobopsis*) *cylindricus* clade (hereafter COCY species) lack metapleural glands. (The informal subgenus *Colobopsis* appears to be a heterogeneous group, and this classification could change.) However, in most of these taxa, mandibular gland (MG) reservoirs have hypertrophied through the abdominal tip to fill much of the body cavity. Their products include phenolic acetogenins and/or diterpenes, as well as sugars that convey adhesive properties to the secretions (Jones et al. 2004). All of these components are nitrogen-free. Some of the phenolic acetogenins, i.e., the corro-

sively irritant m-cresol and resorcinol, possess known antiseptic activity, and others should be at least weakly antiseptic by virtue of their weak acidity. All COCY taxa forage by 'grazing' microscopic foods from adaxial leaf surfaces, mainly in the high canopy (Davidson et al. 2004), and they nest both polydomously, and wholly or partly within cavities of live trees. Canopy nesting is basal in the group, and a more derived trait is nesting low (0–3 m) in live trunks only. The most derived nesting habit includes both central nests in live trunks and satellite nests in dead wood. In four of five members of this last group, m-cresol is a prominent component of MG product. We expect that nest cavities in the arid canopy should be less pathogen-plagued than those in the wet understory, and that nests in fallen wood on the damp forest floor should pose the greatest threat from pathogens by offering conditions conducive to their growth. Densities of wood, and of root- and butt-rot cavities, should also be greater in the understory than in the canopy, and an ability to nest in dead wood should provide the greatest density of potential nest sites. To the extent that nesting space is limited, such limitations could have driven evolution of the capacity for increased use of pathogen-plagued nests.

Given the observed phylogenetic trend in COCY species' nesting habits, known antiseptic properties of MG compounds, and the desirability of defining mechanisms contributing to nest hygiene, we decided to assess microbial nest associates directly by comparing their presence in COCY-occupied versus unoccupied artificial nests. Opportunistically, we also sampled artificial nests colonized by non-COCY species and a few natural COCY nests in decaying wood. Cultured microbes from surface-sterilized nest wall fiber and carton shelving were preserved and identified by molecular sequencing using oligonucleotides targeting bacteria and fungi. In focusing on the subset of microbes culturable under a particular set of conditions and detectable with universal bacterial and fungal primers, we could have missed some regular microbial associates of the ants. However, our methods were chosen as a simple first approach to probing for regular relationships between ants and microbes in nesting environments where microbial diversity could be high. Studied in this experimental context, consistent over-representation of particular microbes within occupied nests can be related to ant nesting habits, to glandular chemistry (reported here for an expanded set of COCY species), and to known characteristics of the microbes in question.

Two other sets of observations complement the study of nest microbes. First, after opening both occupied and unoccupied nests for microbial sampling (authors' unpubl. data), we measured cavity wall pH. Motivating this measurement was variation in pH-dependent colors of ant MG products (Jones et al. 2004), and the observation that workers of one species applied MG products to plastic nest tubs in the laboratory. Nest wall pH was hypothesized to vary in relation to product color, and to potentially influence microbial affiliations with nest walls. Second, to the extent that ant occupancy of nests in live host trees may depend on establishment of appropriate microbial environments, we suspected non-random use of host trees. We therefore compared frequencies of host use against representation of plant families and genera in the data base of KBFSC tree plots. Working in a protected area, we could not follow these studies with destructive sampling of live hosts trees for microbes.

MATERIALS AND METHODS

Chemistry of Mandibular Gland Products

For taxa whose MG chemistry had not previously been studied, whole worker

ants were collected from individual colonies into approximately 0.5–1.0 ml of methanol and returned to laboratories at the Universiti of Brunei Darussalam (UBD) and the Virginia Military Institute (VMI) for analysis of supernatant by gas chromatography/mass spectrometry (GC/MS) Analytical methods were identical to those in an earlier publication reporting volatile chemistry of nine species (included here from Jones et al. 2004). Peaks were identified by comparison with coinjected compounds from commercial sources or synthesized by T. H. Jones at VMI.

Nest Construction and Sampling

In November-December 2005, two investigators (CRB and DWD) constructed 55 compositionally identical nests, and transported them in the field over five successive days in early December. Each nest consisted of a 2″ × 2″ piece of medium density dipterocarp lumber, approximately 42 cm long and sawn initially into three segments. With a power drill and a stout bit, we drilled two adjacent holes completely through the middle segment (from both ends and meeting in the center) and again, most of the way through both upper and lower segments. The same drill bit was used to eliminate partitions between adjacent holes. The three nest segments were tightly reassembled using wood glue and staples, and a hammer and nail (subsequently removed) were employed to make a single entrance hole near the top of the cavity in the upper nest segment. At points below and above the nest cavity space, intact nests were nailed to 1-m-tall stakes for insertion into the ground. Before nailing, both nests and stakes were given two coats of green, oil base paint, and nests were numbered with permanent marker. Numbered nests were matched haphazardly to colonies of different ant species and were placed either immediately adjacent to natural nests (N = 25) or a short distance (5–7 m) away, but connected by ropes along which workers readily commuted (N = 30). Four nests lacked stakes; two of these were tied directly to tree trunks, and two others, to canopy branches accessible from a walkway. Nests were placed near colonies of all but two COCY spp. known from KBFSC, though sample sizes were uneven and depended on species abundance.

To test for differences in nest-wall pH, we first verified neutral pH of test strips (colorpHast, Merck KGaA, Darmstadt, Germany) in tap water (= stream water) and then held wet strips against the cavity wall until their colors had ceased to change (usually < 1.5 min).

After sampling three COCY-colonized nests with large colony fragments in March–April, 2006, we retrieved nests and sampled microbes of both occupied and unoccupied nests at intervals of 4–6 months: in November–December 2006, July 2007, and November–December 2007. (The few samples from this last period were mostly unusable, perhaps because lab alcohol had been diluted.) Nests appearing to house few ants in early censuses were left for subsequent sampling periods. Harvesting occurred at night, with ants inactive and sealed inside; nests were returned to the KBFSC laboratory for processing. One or two days after sampling, nest segments were disassembled on an isolated table. Live workers and brood were brushed, usually without exploding, into one or more plastic tubs, ringed along their internal lips with an aqueous suspension of poly(tetrafluoroethylene), and covered with lids punctured for aeration. Individual nests were fractured into their original three segments, and nest fiber was extracted from the upper portion of the lowest nest segment; if present, brood were found most dependably in this segment. Selection of fiber lining the nest cavity was otherwise haphazard, and that of carton (falling from nests as ants were extracted), completely haphazard. Given such minimal sampling within nests, we would only expect to see microbial taxa occurring regularly across

samples if those taxa were very common and widespread within as well as across nests, and such taxa could occasionally be missed. For the few natural dead wood nests sampled, microbial sampling was similar, except that sites for sampling of nest lining (fiber) and carton were chosen haphazardly from within brood chambers. Carton and fiber samples were preserved separately in haphazardly selected and subsequently labeled 50-mm centrifuge tubes, washed recently in dilute sodium hypochlorite and then rinsed with tap water and air-dried. For nests lacking carton (unoccupied nests, some nests housing non-COCY species, and COCY nests lacking brood), only fiber samples were available. Live ants were fed honey water until their return to the field with reassembled nests, and some nests were sampled again on successive field trips. On the second through fourth field trips, various colony fragments were retained for observation.

After extracting samples, we sterilized a plexiglass chamber ("sterile hood"), approximately 36 cm on a side, with a tightly-fitted door. Internal chamber walls were swabbed with Kimwipes© soaked in 10% sodium hypochlorite and then 95% ETOH, which quickly dried them. Using a sterile razor blade, we haphazardly cut tiny fragments of nest wall fiber or carton samples and placed them individually by nest number and sample type into 1.5-ml microcentrifuge tubes containing 10% sodium hypochlorite for surface sterilization. (Forceps used to handle samples were sterilized in the flame of an alcohol lamp.) Subsequent sample agitation for 2 min was followed by two sequential 2-min rinses (with agitation) in microfuge tubes filled almost to capacity with sterile, deionized water. After drying on sterile filter paper inside the chamber, samples were transferred to small (50-mm diameter) sterile plates of Malt Extract Agar (MEA) and plated three per plate and widely separated. Taped plates were transferred to a second and identical "sterile hood" covered externally in aluminum foil to exclude light. Plates were checked daily, and when microbial growth around individual plated samples almost met that from other fragments, cultured microbes were harvested using sterile forceps, and with underlying agar, into 95% ETOH. Samples within a plate usually grew visually similar cultures; if so, such samples were combined. If microbial cultures within a plate differed in appearance, these were preserved individually. All preserved samples were returned to Utah for DNA extraction (below).

Sampling of Leaves and Roots

As the study progressed, it became clear that certain prominent nest microbes had previously been reported as endophytes, so we also sampled and identified endophytes from accessible resource plants. Although all COCY species forage principally in the canopy, workers from certain colonies also regularly grazed leaves of a few understory plants, and one heavily used tree canopy was reachable from a canopy walkway. We observed workers of species 'YG' and 'SA' in the understory, and of 'LE' in the canopy, and circled (in permanent ink) 'leaf-stops' where foragers paused to graze adaxial leaf surfaces. Because the endophytic microorganisms in question can also be root parasitic, we sampled shallow roots of understory resource plants used consistently by colonies of 'BBQ', 'YG', and nrSA. Sampling of leaf and root tissues from COCY resource plants was exploratory and not sufficiently replicated to test hypotheses of ant association with particular endophytic microbes in the foraging territory. Whole leaves or bits of root tissue were harvested and bagged individually in new plastic zipper-sealed bags and returned to the KBFSC laboratory for surface-sterilization and culturing using techniques identical to those for nest fiber and carton.

DNA Extraction, PCR, Sequencing, and Microbial Identifications

DNA extraction was carried out using Qiagen's DNeasy® Tissue Kit (QIAGEN®, Valencia, CA), following manufacturer's specifications for the Purification of Total DNA from Animal Tissues (Spin-Column Protocol), though modifying step one. That step (tissue shredding and grinding), was carried out in a 1.5 ml microfuge tube after first freezing a portion of the sample in liquid nitrogen. PCR amplifications utilized universal primers for the bacterial 16S rRNA gene (27f, 5'-AGAGTTTGATCC TGGCTCAG and 1492r, 5'-GGTTACCTTG TTACGACTT) and the fungal 18S rRNA gene (nu-SSU-0817, 5'-TTAGCATGGAA-TAATRRAATAGGA and nu-SUU-1536, 5'-ATTGCAATGCYCTATCCCCA). A 2-µl DNA sample was added to a 42.3 µl reaction mixture consisting of 11.2 mM Tris-HCL (pH 8.8), 59 mM KCL, 0.38 mM dNTP mix, 1.5 mM MgCl2, 0.5 µg BSA, 0.38 µM of each primer, and 2 U Taq DNA Polymerase. PCRs were carried out on a MiniCycler™ PTC-150 (MJ Research Inc., Watertown, MA), with published protocols slightly altered to decrease false priming. The amplification protocol for bacterial primers typically consisted of a denaturing step of 95°C for 2 min, followed by 35 cycles of 90°C for 45 sec, 50°C for 45 sec, and 72°C for 1.5 min; it concluded with a final extension step at 72°C for 7 min. With fungal primers, the protocol typically consisted of a denaturing step of 94°C for 3 min, followed by 35 cycles of 94°C for 1 min, 56°C for 1 min, and 72°C for 1 min; it concluded with a final extension step at 72°C for 10 min. PCR products were purified using Qiagen's QIAquick®PCR Purification KIT, and following the manufacturer's protocol for use of a microcentrifuge.

PCR amplicons were sequenced directly using ABI dye-terminator chemistry at the DNA Core Facility, University of Utah School of Medicine. Forward and reverse sequences were assembled and edited using Sequencher v 4.5 (GeneCodes 2005). Related sequences were aligned in ClustalX (2.0) to check variable positions and make minor adjustments. Consensus sequences were entered into BLAST (National Center for Biotechnology Information-GenBank) for identification. We present mainly genus-level identifications; species level determinations are tentative due to occasional availability of just partial sequences (typical for environmental samples), and to limitations of the BLAST data base for gene regions studied.

Ant-host Associations

During two research trips, we cut, pressed, and dried vegetative material from accessible live COCY species' host trees along approximately 2.8 km of the Ashton and upper Enkiang trails; not all nest trees were found. Material was identified to genus, and occasionally to species, at the Brunei Herbarium. Representation of plant families and genera among sampled hosts was compared to that summed from three tree plots maintained by KBFSC and located along the same trails.

Statistical Analyses

All analyses were done in JMP version 4.0.4 (SAS Institute 2001). Conservatively, where multiple microbes were present but inseparable without cloning (one case each for fungi in COCY fiber and carton samples), focal nest associates were considered to be absent.

RESULTS

Mandibular Gland Chemistry

Augmenting published data, Table 1 summarizes the volatile chemistry of mandibular gland products for the eight COCY species colonizing artificial nests. Pending comparisons of collections with type specimens, just one (*Camponotus* [*Colobopsis*] *saundersi*) has been identified to species,

Table 1. By species, percentage representations of compounds (including fatty acid methyl esters) in mandibular gland (MG) products; t = trace. See text and Jones et al. (2004) for details. Data are listed by voucher numbers (DWD KB collection series) and species acronyms (from Cook 2008). Product colors are identified below: w = white; y = yellow; o = orange; r = red (occasionally pink or peach).

	Species							
MG product	05B-50 'LE'* (r)	02-118 'RHYG' (y)	02-108 'YG' (y)	07B-T2 'ICY' (w)	11-Feb 'CL' (w)	Feb-64 'AR' (w)	02-21 'SA' (w)	05A-37 'nrSA'[1] (w)
Phenolics								
m-Cresol (**1**)					14		1	37.5
Resorcinol (**2**)	10							
6-Methylsalicylic acid (**3**)[2]					30			7.5
2,4-Dihydroxy-acetophenone (**4**)	25		1		3	4	75	3.2
2,4,6-Trihydroxy-acetophenone (**5**)	1.8		2			15		
2-Methyl-5,7-dihydroxy-chromone (**6**)		24	21			1		
Orcinol (**8**)						t		
Terpenoids								
Citronellal								
Citronellol								
Citronellic acid								t
Isopulegol								
(6R)-E-2, 6-Dimethyl-2-octen-1,8-dioic acid (**9**)						44		16.5
E-8-Hydroxy-3, 7-dimethyl-6-octenoic acid (**10**)						t		

[1] Means of two analyses for same species.
[2] In insects, compound **3** can be an intermediate in the production of **1** (Birch and Donovan 1953).

and most COCY species are unidentified or undescribed. The remaining collections are referenced by descriptive acronyms and voucher numbers (see Acknowledgements). Compound numbers correspond to those in Jones et al. (2004); we omit previously reported aliphatics occurring just in ant gasters, and therefore not MG products (authors' unpublished data). One or more of several phenolic acetogenins (compounds **1–6**) and terpene diacids (**9–10**) occur in each colonizing species. Corrosively irritant m-cresol (**1**) is a major component in several derived species (Table 1 vs. Cook 2008). None of the sampled COCY species failing to colonize artificial nests possesses significant quantities of m-cresol in MG products (Jones et al. 2004 and T.H. Jones, unpublished data), nor do those taxa maintain satellite nests in fallen wood (Cook 2008 and authors' unpublished data).

Three of the polyacetate-derived aromatics (compounds **4–6** in Table 1 below), at least one of which occurs in each species, determine the bright colors of MG products (Table 1, Jones et al. 2004). Independently of which product predominates, these colors are pH-dependent in the range of 5.6 (white) to 7.8 (pink or red), and cream-to-yellow or orange at intermediate pH (Jones et al. 2004).

Nest pH and Occupation

In preliminary trials, and contrary to expectation, nest wall pH was invariant (≈ 4) over all early sampled nests with and without ants, as well as in natural nests in preliminary trials. Among ant-occupied nests were those used by COCY species with MG products ranging from white ('CL' and 'SA') to yellow ('YG'), and red ('LE'), one nest each for *Camponotus* species 06B-04 and *Tetramorium* sp. 06B-05 (a myrmicine ant). Based on lack of variation in pH, we eventually discontinued measurements.

Within 18 months (usually sooner), COCY species had colonized 44% of the

25 nests located adjacent to nests of known colonies, and 48% of those not colonized by other species (*Polyrhachis* and *Tetramorium*). Six of eleven uncolonized nests were located near natural nests of taxa not known to inhabit natural fallen wood (see Cook 2008), and several others had been breached by water. Of 30 artificial nests placed 5–8 m from natural nests in a major foraging direction, COCY species occupied 33.3%, or 34.5% of nests not occupied by other taxa. Eleven of the uncolonized nests in this set were stationed near species not known to nest naturally in dead wood, and some others had been breached by water or disturbed by sandalwood poachers. Both 'LE' and 'YG' moved into artificial nests (the latter species with brood), despite apparently not nesting naturally in fallen wood. Not all COCY-occupied nests were sampled for microbes, because some had been colonized by just small colony fragments.

Microbes in Nest Wall Fiber

Six COCY species colonized artificial nests and/or were harvested from natural nests, and microbes from these two nest types were lumped in subsequent analyses. For 24 fiber samples from COCY nests, replicate PCRs failed to yield 'hits' in ten cases with universal bacterial primers but in just three cases with universal fungal primers. Comparable data for 17 unoccupied nests were seven and three, respectively, and for carton samples, were seven and zero of 24 samples. The acidic environment of nest cavity walls may generally favor fungi over bacteria, but we cannot rule out influences of culture conditions specific this study, or of differentially 'successful' PCRs.

In Table 2, microbial data are presented with COCY species organized by nesting habits. Workers of all fallen wood nesters commute extensively on the ground, in contact with soil microbes. So far as is known, both 'YG' and 'RHYG' nest only in live trees, but the two taxa differ in exposure to soil microbes. 'YG' has extensive contact with leaf litter and soil, whereas observations of four different colonies reveal 'RHYG' commuting along dead and live stems, rather than over leaf litter or soil. Both nesting and foraging in the canopy, 'LE' has the least exposure to soil microbes, except as those organisms inhabit decaying leaf litter in the canopy itself.

For the most common fungal and bacterial taxa, Table 2 reports microbial data by colony, nest sample (including multiple nests per colony), and total nest samples over time (including replicate samples from individual artificial nests). Representatives of one bacterial genus and one fungal genus appeared repeatedly in both nest fiber and carton from COCY species' nests. These were, respectively, *Burkholderia* and *Trichoderma* (anamorph = asexual form)/*Hypocrea* (teleomorph = sexual form). GenBank accession numbers are in three sets: GQ306157-GQ306183 (file Anderson_*Burkholderia*.sqn), GQ332537 (file Anderson_*Burkholderia*.sqn), and GQ306184-GQ306202 (file Anderson_*Hypocrea*.sqn).

Only microbes from fiber can be compared with those from unoccupied nests, which lacked carton. At the colony level, over-representation in association with COCY is clearest for *Trichoderma* species, which were detected in nests of 50% of 14 COCY colonies and 70% of ten colonies from taxa nesting regularly in dead wood. (In nest carton, they were found in 69% of 13 colonies and 70% of ten colonies nesting in dead wood.) In contrast, members of this genus were detected in none of 17 unoccupied nests, and in just one of seven nests inhabited by other ant taxa. Presence of *Trichoderma* differed significantly across the three nest types in nominal logistic regression ($\chi^2_{[2]} = 13.96$, $P < 0.0009$, $N = 38$). Nevertheless, it could be argued that nests of COCY species were sampled more thoroughly than were other nests, due to our sometimes having sampled fiber from multiple nests per colony, and/or individ-

Table 2. Occurrences of the most common bacterial and fungal genera detected in artificial nests at KBFSC. Sample sizes are in parentheses for N = numbers of colonies (some sampled by multiple nests, and some nests sampled repeatedly), numbers of nests (independent nests, but sometimes more than one per colony), and total nest samples (including repeat samples of nests restored and returned to the field).

Species	– *Burkholderia* spp.[1]			– *Trichoderma* spp.[2]		
	Colonies sampled N	Nests sampled N	Total nests over time N	Colonies sampled N	Nests sampled N	Total nests over time N
NEST WALL FIBER						
COCY spp. Nests						
Satellite nests in dead wood						
'nrSA'	1 (1)	1 (1)	1 (1)	1 (1)	1(1)	1 (1)
'SA'[3]	3 (4)	3 (6)	3 (6)	1 (4)	1 (6)	1 (6)
'AR'	1 (2)	1 (3)	1 (4)	2 (2)	2 (3)	3 (4)
'CL'	2 (2)	2 (2)	2 (2)	2 (2)	2 (2)	2 (2)
'ICY'[4]	1 (1)	2 (4)	2 (4)	1 (1)	1 (4)	1 (4)
No satellite nests in dead wood						
'RHYG'[4]	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (0)
'YG'	1 (2)	1 (3)	1 (4)	0 (2)	0 (3)	0 (4)
'LE'	0 (1)	0 (1)	0 (2)	0 (1)	0 (1)	0 (2)
Unoccupied nests						
All	5 (17)	5 (17)	5 (17)	0 (17)	0 (17)	0 (17)
Nests occupied by non-COCY spp.						
Tetramorium sp. KB06B-05	1 (1)	1 (1)	1 (1)	0 (1)	0 (1)	0 (1)
Camponotus sp. 1 KB06B-04	1 (3)	1 (3)	1 (3)	0 (3)	0 (3)	0 (3)
Polyrhachis [*Polyrachis*] sp. KB07A - 02	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
Polyrhachis sp. 1	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)
Polyrhachis sp. 2 (*hector* group) KB07A-03	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	0 (1)
CARTON NEST SHELVING						
COCY spp. Nests						
Satellite nests in dead wood						
'nrSA'	1 (1)	1 (1)	2 (2)	1 (1)	1 (1)	1 (2)
'SA'	4 (4)	5 (6)	5 (7)	1 (4)	1 (6)	1 (7)
'AR'	1 (2)	1 (3)	1 (4)	2 (2)	2 (3)	2 (4)
'CL'	1 (2)	1 (2)	1 (2)	2 (2)	2 (2)	2 (2)
'ICY'[4]	0 (1)	0 (2)	0 (2)	1 (1)	2 (2)	2 (2)
No satellite nests in dead wood						
'RHYG'[5]	0 (1)	0 (1)	0 (1)	1 (1)	1 (1)	1 (1)
'YG'[5]	0 (1)	0 (2)	0 (5)	1 (2)	1 (2)	1 (5)
'LE'	0 (1)	0 (1)	0 (2)	0 (1)	0 (1)	0 (2)
Non-COCY spp.						
Camponotus sp. 1[5]	1 (3)	1 (3)	1 (3)	0 (3)[5]	0 (3)[5]	0 (3)[5]

[1] BLAST hits included *Burkholderia* spp.: *tropica* (most common), 'SA', *ginsengisoli* (in GenBank as *koreensis*, not a legitimate name), 'SA', *phenazinium*, *Polyrhachis* sp. 1, and *terrae*-like CL; hits for a nest occupied by *Camponotus* sp. 1 were near *uraane* and *nodosa*.

[2] BLAST hits included *Trichoderma* spp. or *T. viride* (anamorph) and *Hypocrea lutea* (identifications to be checked by I. Druzhinina).

[3] In one sample of SA fiber and one sample of *Camponotus* sp. 1 carton, multiple fungal taxa not discriminated without cloning; *Trichoderma* cannot be ruled out.

[4] Three of four sampled ICY nests were natural and in fallen wood on the forest floor; one natural nest possessed both *Burkholderia* and *Trichoderma*, and *Burkholderia* alone was found in a second natural nest. The sole sampled 'RHYG' nest was in a recently dead, standing host.

ual nests repeatedly over time. To circumvent this problem, we repeated our analysis including data from just the first of replicate samples of individual nests, and also classifying *Trichoderma* as absent from half the colonies where it was found in just half of all replicate nests per colony. Even in this more conservative analysis, *Trichoderma* was over-represented in COCY nests (35.7% of samples) relative to the other two nest types from which it was either absent or rare ($\chi^2_{[2]} = 9.16$, $P = 0.01$, $N = 38$).

Among COCY taxa, *Trichoderma* was detected exclusively and significantly more often in species nesting regularly in fallen wood on the forest floor (Table 2; $\chi^2_{[1]} = 7.19$, $P = 0.007$, $N = 14$). All but one of those taxa ('AR') produce m-cresol as a component of MG product; as a fraction of total volatiles, m-cresol is least well represented in 'SA' (Table 1), and detection of *Trichoderma* was also least consistent in nests of that species.

Burkholderia bacteria were detected in 64.3% of 14 COCY spp. nests but were also found in smaller percentages of both unoccupied nests (29.4%) and nests housing other ant taxa (42.9%). At the colony level, the bacteria were not statistically over-represented in COCY nest fiber in the less conservative analysis ($\chi^2_{[2]} = 3.85$, $P = 0.15$, $N = 38$). However, *Burkholderia* were detected marginally more frequently in (lumped) ant-occupied nests than in vacant nests ($\chi^2_{[1]} = 2.98$, $P = 0.08$), and they were significantly more common in COCY nests than in unoccupied nests ($\chi^2_{[1]} = 3.84$, $P = 0.05$, $N = 31$). When each of these three analyses was repeated with a more conservative data set (modeled on that for *Trichoderma* above), none was statistically significant ($P \gg 0.05$ in each case). Finally, lumping COCY species in each category, *Burkholderia* was more common in nest fiber of taxa regularly inhabiting fallen wood, than in other taxa ($\chi^2_{[1]} = 3.74$, $P = 0.05$, $N = 14$).

In nest fiber, *Burkholderia* and *Trichoderma* co-occurred significantly more often at the level of ant colony than predicted by chance ($\chi^2_{[1]} = 3.94$, $P < 0.05$, $N = 13$, in nominal logistic fit with the equivocal nest with multiple fungi omitted). Based on their separate rates of detection in COCY colonies, independence would have predicted co-occurrence in 41.3% (64.3% × 64.3%) of nests. However, *Trichoderma* was present in 85.7% of nests in which *Burkholderia* was confirmed, and *Burkholderia* in 75% of nests where *Trichoderma* was detected. After removing the four colonies of taxa nesting naturally only in live wood, the relationship is no longer significant ($P \gg 0.05$, suggesting that it depends largely on differences in species' nesting habits. Identical comparisons for carton samples revealed no evidence of association between the two categories of microbes, mainly because *Trichoderma* was absent altogether from 'SA' (little m-cresol) carton, despite presence of *Burkholderia* in almost all such samples (Table 2).

Endophytic Fungi of Leaves and Roots

Endophytic *Trichoderma* were documented in two of three leaves and one of three roots sampled. One of the two positive determinations for leaves was for a canopy host and resource plant of 'LE', and the other was from an understory resource sapling of 'SA'. *Trichoderma* was not detected in an understory palm utilized heavily by 'YG'. *Burkholderia* were detected in none of three leaves, but in one of three roots, sampled; that single root was from an understory resource plant of 'BBQ', the sister species of 'LE' (Cook 2008), but a species commuting regularly on the ground. *Trichoderma* was detected in that same root.

Ant Associations with Host Trees

Both individually and as a group, COCY species nested in a diversity of live host species (Table 3). Several host taxa possessed extrafloral nectaries (EFNs), producing food rewards for ants on leaves or reproductive structures (*Ixora* fruits), but

most host species did not. Across all ant taxa, and despite lack of species-specificity in ant-host associations, certain taxa lacking EFNs were overrepresented as hosts relative to their family and genus level abundances in forest plots. Accounting for ~ 21% and ~34% of 56 identified hosts, respectively, both Fabaceae and Phyllanthaceae were statistically overrepresented relative to 'other plant families' from which hosts had been identified (Likelihood Ratio [LR] $X^2_{2,\ 2458} = 8.08$, $P = 0.0030$ for Fabaceae, and LR $X^2_{2,\ 2458} = 13.87$, $P = 0.0002$ for Phyllanthaceae). Two thirds of hosts in the Fabaceae were species of *Fordia*, but because *Fordia* also comprised 70% of all family members in tree plots, it was actually significantly under-represented as a COCY host tree (LR $X^2_{1,\ 215} = 8.01$, P = 0.0047). *Antidesma* and *Cleistanthus* were approximately equally represented as hosts and together accounted for 89.5% of the Phyllanthaceae. Each was significantly over-represented as hosts compared to the distribution of abundances as a whole (focal genus versus lumped other genera: LR $X^2_{1,\ 99} = 36.47$, $P < 0.0001$ for *Antidesma*, and LR $X^2_{1,\ 215} = 14.16$, P = 0.0002, for *Cleistanthus*).

DISCUSSION

Frequent colonization of artificial nests (~38% overall) suggests that suitable living space is limiting for polydomous COCY species and other cavity-nesters at KBFSC, perhaps especially so for taxa in which workers lack metapleural glands (all but *Tetramorium* in Table 2). Uniformly low pH of nest cavity walls is likely determined by brown-rot wood decay fungi (e.g. Humar et al. 2001) and, consistent with our data, may generally favor fungi over bacteria (e.g. Bot et al. 2002). Experimental data also reveal over-representation of *Trichoderma* fungi in artificial nests colonized by COCY taxa regularly maintaining satellite nests in fallen wood; four of these five species are the only taxa possessing m-cresol as a MG product. Although *Burkholderia* bacteria were detected most frequently in COCY species' nests, they were overrepresented there only in relation to unoccupied nests, and only in the least conservative analysis. Below, we review these results in the context of a phylogeny of COCY species (Cook 2008), ant habits, and known attributes of *Trichoderma* and *Burkholderia*.

Nest Site Limitation

Overall, evidence for limitation of nest space is consistent with phylogenetic data suggesting that shortages of cavity space could have driven progressively greater use of understory nests and, eventually, nests in fallen wood, as the increasingly derived character states (Cook 2008). Because nests were placed adjacent to known colonies, high rates of colonization by COCY species are due partly to high discovery rates, but they also indicate that suitable nesting space was limiting for many of these colonies. Colonization rates might have been higher still, had we sampled just taxa known to nest in the understory. For other species, artificial nests positioned at bases of host and resource trees may have been unacceptable despite substantial worker traffic to the understory and on the ground. Additionally, in 'RHYG', which nests throughout trunks of small trees, nesting space may not be limiting until death of the host tree, which it regularly kills (authors' unpublished data). Finally, both 'YG' and 'LE' adopted artificial nests despite not nesting naturally in fallen wood.

To the extent that ants procure food from their hosts, limited nest space may correlate with food limitation. A minority of hosts provide extrafloral nectar (Table 3), and frequent mortality of 'RHYG' host trees suggests that this species drains resources from live hosts, despite not tending trophobionts inside. Trunks are gradually hollowed out, and bark is stripped from external surfaces where workers harvest cambial heteroplasias at sites of injury. Similar behavior is reported

Table 3. Ant-host associations: entries are numbers of occurrences. Not all hosts were located. Asterisks mark taxa with extrafloral nectaries.

Ant sp.	'SCY'	'nrSA'	'SA'	'AR'	'CL'	'RHOG'	'LCY'	'YG'	'RHYG'	'BBQ'	Not recorded
Plant Family and Genus											
Anacardiaceae											
Gluta							1				
Celastraceae											
Lophopetalum									1		
Dipterocarpaceae											
*Shorea**			1								
Euphorbiaceae											
*Blumeodendron**							1				
*Macaranga (hullettii)**			1								
*Mallotus**			2		1						
Fabaceae											
*Albizia**									1		
*Archidendron**			1							1	
Fordia			1	3	3				1		
Callerya										1	
Meliaceae											
Aglaia											1
Myristicacae											
Horsefieldia				1							
Myrtaceae											
Memecylon			1								
Syzigium								1			
Oleaceae											
*Anacolosa**						1					
Phyllanthaceae											
Antidesma			5						3	1	
Aporosa					1						
Cleistanthus	1		4				1		2		
Drypetes									1		
Polygalaceae											
Xanthophyllum					1		1				
Rubiaceae											
*Ixora**		1	1								
Praravinia					1						1
Sapindaceae											
*Pommetia**								1			
Simaroubaceae											
Eurycoma			2								
Tiliaceae											
Microcos				1							
Violaceae											
Rinorea				1							

* Hosts with EFNs

for *Camponotus* [*Colobopsis*] *quadriceps* (Davidson and McKey 1993), a phytoecious resident of *Endospermum* (Emery 1925), and a New Guinea relative of COCY species. In other species, very high worker activity can occur throughout the day at some dead wood nests lacking brood ('CL'). Finally, space could be associated with food in the form of nest shelving. In lab-housed colony fragments, workers of various COCY species deposited liquid from sugar-soaked cotton balls on carton fragments reserved from nests and supplied to the ants. Initially dry and fibrous, the carton even-

tually turned dark black, whereupon workers harvested the loose black material, leaving dry fibrous carton of diminished thickness.

Ant-microbe Associations

Remarkably, even light sampling of cultured microbes from few colonized nests revealed representatives of one bacterial genus (*Burkholderia*) and one fungal genus (*Trichoderma*) as frequent nest associates of COCY species. *Trichoderma* species, filamentous Ascomycota (Hypocreales, Hypocreaceae) were cultured mainly from COCY species' nests. Because nests were assigned haphazardly to field locations, this result cannot be explained by preexisting endophytic infections of lumber used in nest construction. Presence of *Trichoderma* and *Burkholderia* in a nest occupied by *Polyrhachis* (informal subgenus *Polyrhachis*) workers is noteworthy, given that members of this group share and defend territories with COCY species (Davidson et al. 2007). Although these species nest in soil, where they line cavity walls with wood fiber (changed out periodically), they can maintain 'pavilions' without brood in standing dead wood (authors' unpublished observations).

Across COCY species, *Trichoderma* was detected in nest fiber of just the five taxa regularly maintaining satellite nests in fallen wood (Table 2), and four of these taxa produce *m*-cresol as a component of MG product (Table 1). The exception is 'AR', where the major component is a diterpene (**9**). Comparing the four taxa with *m*-cresol, frequency of *Trichoderma* was lowest in 'SA', coincidentally the species with the lowest concentration of this compound (1–5% across repeat samples, versus 30–98%, respectively, Table 1, and authors' unpublished data). In carton, *Trichoderma* was detected at least once in all COCY taxa except 'SA' and 'LE', the canopy-restricted species. Together, these data suggest that *m*-cresol may favor *Trichoderma* over other fungi (see below). Although certain categories of diterpene acids also exhibit strong antifungal activity (Kopper et al. 2005), the response of *Trichoderma* to such compounds remains unexplored.

To account for distributions of *Trichoderma* and *Burkholderia* across artificial nests, we propose the following hypothetical scenario, consistent with our data and ancillary observations. Widespread in soils (Coenye and Vandamme 2003), or in soils and decaying wood (e.g. Kubicek and Harman 1998), members of both genera may first have colonized artificial nests via passive dispersal on tarsi of ant taxa commuting regularly over the ground. (COCY species do not actually forage in leaf litter.) The same microbes may not have been picked up in abundance by species with activities confined to vegetation, nor might *Trichoderma* have thrived in nests of terrestrially commuting taxa lacking sufficient *m*-cresol to convey a competitive advantage to these fungi (which degrade the compound; e.g. Bruce and Highly 1991 and Atagana et al. 2002; Karetnikova and Zhirkova 2005) over other fungi. (Evidence also indicates that *Burkholderia* can use *m*-cresol and other aromatics as carbon sources [e.g. Shields et al. 1995; Caballero-Mellado et al. 2007]). MG products could have arrived at nest walls via their volatility or been applied as nest wall fiber was stripped and macerated into carton shelving. Similar 'arrival and survival' characteristics of *Burkholderia* and *Trichoderma* have could have contributed to their positive association in nest fiber.

Clearly, our simple approach to microbial sampling could have missed other common associates of the ants, e.g. taxa concentrated in other parts of the nest, or more readily cultured on other media. (However, samples plated onto methanol and acetate agars during one sampling period typically yielded the same organisms as did cultures on MEA). Additionally, plate cultures are not unbiased methods for environmental sampling but favor taxa

requiring high rates of resource supply (see below), which central-place foraging ants may nevertheless provide.

Potential Benefits of Association with Microbes

Both *Burkholderia* and *Trichoderma* have also been isolated from nests of leaf-cutter ants (Attinae), with the former genus reported to have antibiotic activity against entomopathogenic fungi (Santos et al. 2004), and the latter to be commensals or mild parasites of the fungus garden (Currie et al. 1999a; Bot et al. 2002; Rodrigues et al. 2008). Although as mycoparasites, *Trichoderma* may damage attine fungal gardens, they are beneficial in human agriculture where they are exploited commercially as biological control agents (e.g. Kubicek and Harman 1998) that arrest growth of wood decay fungi and plant pathogens. We speculate that *Trichoderma* could play a similar role in nest hygiene by protecting COCY workers and brood from entomopathogenic fungi and bacteria. A subset of the mechanisms by which *Trichoderma* fungi control plant pathogens (Kredics et al. 2003; Howell 2003) could directly harm nest pathogens. If nests in live hosts also contain these fungi, other mechanisms could potentially modify anti-pathogen defenses of live host trees to the ants' advantage. Modes of action include: (a) endogenous and exogenous production of chitinolytic enzymes that degrade the polysaccharides, chitin and β-glucans conveying rigidity and integrity to fungal cell walls; (b) production of proteases that inactivate hydrolytic enzymes of pathogenic fungi, breaking them down to peptides and amino acids so that fungi cannot invade host tissues; (c) competitive replacement of fungal pathogens within plant tissues; (d) production of antibiotics; (e) synergistic actions of chitinases with both antibiotics and proteases; (f) metabolism of spore germination stimulants; (g) induction of plant-produced terpenoid defenses, potentially fungitoxic peroxidases, and pathogenesis-related proteins in roots and leaves of live plants themselves, possibly including COCY live host trees. Plant-produced chitinases and proteases should have activities similar to those of comparable *Trichoderma* enzymes. Just the presence of *Trichoderma* in the rhizosphere, contacting but not invading plant tissues, can induce systemic plant defenses that are potentially effective against bacterial as well as fungal pathogens (Harman et al. 2004). Both mycelial growth and enzyme production by *Trichoderma* increase in mesic environments and acidic substrates (Kredics et al. 2003), common conditions in fallen wood on the rainforest floor.

COCY species lack pupal silk, which may protect other ant taxa (e.g. *Polyrhachis* spp.) from nest pathogens and may be especially effective where microbial antagonists of such pathogens are interwoven with silk (e.g. Kaltenpoth 2007, for wasps). With naked pupae, COCY colonies and species not associating with *Trichoderma* must maintain nest hygiene by other means. Laboratory-housed workers of 'YG' colony fragments uniquely deposited abundant MG product on floors and walls of plastic nest chambers, and those of 'LE' lined nest chambers with cotton shredded from *Candida* yeast-occupied sugar-soaked cotton balls offered as food. Both behaviors could be related to nest hygiene. Additionally, from 'SA' nests, we isolated *Verticillium insectorum*, a fungus reported to be parasitic on *Trichia* slime molds (Rogerson and Stephenson 1993), which our primers would not have detected. Like *Trichoderma*, slime molds consume microbes in decaying vegetation.

We cannot presently rule out direct or indirect positive effects of *Trichoderma* infections on food production inside nests and on foraging substrates, or on expansion of nest space. Whether chitinolytic enzymes and proteases are produced by *Trichoderma*, and/or elicited in live host and resource plants, such enzymes might increase resource availability for leaf-graz-

ing ants feeding on products of fungal breakdown. *Trichoderma* propagules could also be among spores digested *in situ* in a worker's infrabuccal cavity to form lipid-rich products (authors' unpublished data, see also Hansen et al. 1999, for *Camponotus modoc*). Further, by stimulating sporulation of some fungi (Brazier 1971), *Trichoderma* might increase spore availability to ants as food. Finally, consistent with saprophytic life styles, *Trichoderma* species possess rich arsenals of extracellular enzymes involved in degradation of cellulose (endo- and exo-glucanases, β-glucosidase, cellobiohydrolase), lignin and hemicellulose in plant cell walls (laccase, peroxidase, xylanase, xylosidase, pectinase and pectin lyase), starch (α-amylase), and chitin (chitobiosidase, N-Acetyl-β-D-glucosaminidase) (e.g. Harman and Kubicek 1998; Kredics et al. 2003). These enzymes could potentially make sugars available to stem-mining or leaf-grazing COCY taxa, just as activities of comparable enzymes subsidize growth of fungal associates of leaf-cutter ants (Gomes De Siqueira et al. 1998; Schiøtt et al. 2008), and cavity space could in the process. Whether *Trichoderma* retard wood decay by mycoparasitism (Shigo 1989; Bruce and Highly 1991; Bruce et al. 2000) or hasten it via cellulolytic activities may depend on species and strain.

Burkholderia bacteria may grow especially well in association with ant waste and perhaps benefit ants through waste recycling. All identified species (footnote in Table 2) belong to the *Burkholderia* clade containing all but one of the plant-associated diazotrophic species, including root-nodulating members in which presence of the nifH gene has been confirmed (Coeyne and Vandamme 2003; Reis et al. 2004; Martínez-Aguilar et al. 2008). Various species in this group produce ureases and grow well aerobically on ammonium substrate (Caballero-Mellado et al. 2004; Reis et al. 2004). If *Burkholderia* recycle COCY species' waste (see also Van Borm et al. 2002, for congeners inhabiting gut pouches of a common KBFSC pseudomyrmecine), this might explain how nest cavity walls remain remarkably free of fecal contamination in nests tightly packed with workers and brood (authors' observations). Where studied, N-fixation by diazotrophic *Burkholderia* occurs under microaerobic conditions (Reis et al. 2004) such as could exist at night in very crowded nests of strictly diurnal COCY species. Both temperature and pH levels in ant nests of the equatorial KBFSC rain forest are in the range in which N-fixation by these species proceeds well (25–37°C, optimum 30°C; pH 4.5–6.5; see Reis et al. 2004).

If *Burkholderia* were to enhance N availability in the nest, this process could potentially contribute to nest longevity. In high lignin substrates like wood, N fertilization favors breakdown of relatively easily decomposed cellulose by a variety of decomposers and leaves behind more recalcitrant lignocellulose (Fog 1988), which fewer microbes can degrade. Time and again, we noted that COCY nest cavity walls in natural fallen wood were remarkably hard and extremely difficult to crack open, despite extensive decay of external wood. Hardening of cavity walls should lengthen the useful life spans of nests in dead wood.

Endophytic *Burkholderia* and *Trichoderma*

Some *Trichoderma* and *Burkholderia* also form sustaining endophytic infections in roots, stems, and leaves (e.g. Bailey et al. 2006; Coenye and Vandamme 2003; Compant et al. 2005a,b). Both taxa typically contact plants in the rhizosphere, where they stimulate upregulation of systemic plant defenses, spread into roots (van Loon et al. 1998; Harman et al. 2004; Compant et al. 2005b; see also e.g. Carroll 1988; Arnold 2003), and can enhance nutrient capture (Caballero-Mellado et al. 2007 for *Burkholderia*). Bacteria disperse to stems and leaves through xylem (Compant et al. 2005b), but many fungal endophytes sporulate in leaf litter and colonize new growth via spore

dispersal by wind and/or insect vectors. Endophytes can potentially protect hosts from pathogen damage (e.g. Redman et al. 2001; Arnold et al. 2003), and this outcome is the motivation for commercial use of mycoparasitic *Trichoderma* in agricultural systems.

Several factors suggest that relationships between COCY spp. and endophytes warrant further study. First, and remarkably given the extraordinary diversity and patchiness of endophytes in tropical vegetation (e.g. Arnold and Lutzoni 2007), our highly inadequate sampling of plant material detected endophytic *Trichoderma* at 'leaf stops' in two of three leaves where ants foraged, and in one of three roots of sampled host/resource plants (none were over-represented host taxa). We could easily have missed both organisms where present, e.g. by failing to target plant parts from which the bacteria have been reported (Compant et al. 2005b). Second, all COCY species forage by 'grazing' adaxial leaves for microscopic rewards (Davidson et al. 2004) that, in addition to epiphylls, could include products mediated by foliar endophytes. Third, COCY species would seem to be ideal spore dispersal agents. In many such species, hundreds-to-thousands of workers commute regularly over the ground between central and satellite nests, and between all nests and both resource plants and pathways into the canopy. Fungal spores are common in buccal pellets, and in more derived species, pellets may be deposited on leaves via a peculiar 'shuddering' behavior (Cook 2008).

Finally, although COCY species do not exhibit species-specificity to host trees, certain plant taxa are over-represented as hosts for the ant clade as a whole, and those taxa do not produce ant rewards (Table 3). If the ants are capable of manipulating microbes in the nest, they may also have evolved to recognize and respond to host endophytes with potential to influence colony success. The fact that both over-represented hosts are members of the Phyllanthaceae (formerly included in Euphorbiaceae, see Wurdack et al. 2004) is interesting in light of findings that the capacity of plant pathogens to infect different host taxa varies inversely with phylogenetic distance (Gilbert and Webb 2007), and that beneficial endophytes may be closely related to pathogens (e.g. Schulz et al. 1999; Wang et al. 2009). Finally, *Cleistanthus* hosts were regularly infected by *Fusarium* (like *Trichoderma* a Class 2 endophyte; Rodriguez et al. 2008) (Hairunizam Hj. Panjang, Plant Pathology Unit, Brunei Agriculture Research Centre, pers. comm.), certain species of which convey resistance to fungal pathogens (Schulz et al. 1999). If that is happening here, *Fusarium*-infected hosts may also afford protection against nest pathogens.

Coda

In the context of ant associations with microbes, it seems possible that the dramatic defense of foraging territory by suicidally exploding ants could have arisen in part as a means of preventing contamination by alien fungal strains or species. As a first step in evaluating this possibility, work is under way to determine the degree to which relationships between ants and *Trichoderma* might be species- or strain-specific. If they are, fungi of different ant species could be competitors of one another, with fungal chemistry possibly mediating ant recognition of alien fungi and eliciting ant behaviors that guard against contamination (e.g. Bot et al. 2001b; Zhang et al. 2007, for attine ants and their fungi). Competition between fungal species or strains might be costly to plants and ants as well as fungi.

ACKNOWLEDGMENTS

Research support was provided by the National Geographic Society and a University of Utah Seed Grant (DWD), a Biology Undergraduate Research Program grant (NFA), and a University of Utah Graduate Research Fellowship (SCC). We thank administrations of KBFSC and UBD for project approval, Brunei's Forestry Department for permis-

sion to collect ants and use canopy walkways, and Joffre Hj Ali Ahmad for identifying host tree material. Hjh Masnah Binti Hj Mirasan, Rodzay Hj Abd.Wahib, and the professional staff of KBFSC facilitated our work in many ways. Jon Seger gave NFA advice on bacterial PCRs and processing sequence data, and generously extended use of lab space and equipment. Roy Snelling was to have identified COCY species and described new taxa as necessary. We dedicate this paper to his memory, in gratitude for numerous identifications facilitating our studies over the past several decades. Voucher specimens reside in the entomology collections of the Natural History Museum of Los Angeles County and at the UBD Biology Department.

LITERATURE CITED

Arnold, A. E. and F. Lutzoni. 2007. Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* 88: 541–549.

———, L. C. Mejia, D. Kyllo, E. I. Rojas, Z. Maynard, N. Robbins, and E. A. Herre. 2003. Fungal endophytes limit pathogen damage in a tropical tree. *Proceedings of the National Academy of Sciences, USA* 100: 15649–15654.

Atagana, H. I., R. J. Haynes, and F. M. Wallis. 2002. Batch culture enrichment of indigenous soil microorganisms capable of catabolizing creosote components. *Water, Air, and Soil Pollution* 141: 233–246.

Bailey, B. A., H. Bae, M. D. Strem, D. P. Roberts, S. E. Thomas, J. Crozier, G. J. Samuels, I-Y. Choi, and K. A. Holmes. 2006. Fungal and plant gene expression during the colonization of cacao seedlings by endophytic isolates of four *Trichoderma* species. *Planta* 224: 1449–1464.

Birch, A. J. and F. W. Donovan. 1953. Studies in relation to biosynthesis: I. Some possible routes to derivates of orcinol and phloroglucinol. *Australian Journal of Chemistry* 6: 360–368.

Bot, A. N. M., C. R. Currie, A. G. Hart, and J. J. Boomsma. 2001a. Waste management in leaf-cutting ants. *Ethology Ecology and Evolution* 13: 225–237.

———, D. Ortius-Lechner, K. Finster, R. Maile, and J. J. Boomsma. 2002. Variable sensitivity of fungi and bacteria to compounds produced by the metapleural glands of leaf-cutting ants. *Insectes Sociaux* 49: 363–370.

———, S. A. Rehner, and J. J. Boomsma. 2001b. Partial incompatibility between ant and symbiotic fungi in two sympatric species of *Acromyrmex* leaf-cutting ants. *Evolution* 55: 1980–1991.

Brazier, C. M. 1971. Induction of sexual reproduction in single A isolates of *Phytophthora* species by *Trichoderma viride*. *Nature New Biology* 231: 283.

Bruce, A. and T. H. Highly. 1991. Control of growth of wood decay basidiomycetes by *Trichoderma* spp. and other potentially antagonistic fungi. *Forest Products Journal* 41: 63–67.

———, R. E. Wheatley, S. N. Humphris, C. A. Hackett, and M. E. J. Florence. 2000. Production of volatile organic compounds by *Trichoderma* in media containing different amino acids and their effect on selected wood decay fungi. *Holzforschung* 54: 481–486.

Caballero-Mellado, J., L. Martínez-Aguilar, G. Paredes-Valdez, and P. Estrada-de los Santos. 2004. *Burkholderia unamae* sp. nov., an N_2-fixing rhizospheric and endophytic species. *International Journal of Systematic and Evolutionary Microbiology* 54: 1165–1172.

———, J. Onofre-Lemus, P. Estrada-de los Santos, and L. Martínez-Aguilar. 2007. The tomato rhizosphere, an environment rich in nitrogen-fixing *Burkholderia* species with capabilities of interest for agriculture and bioremediation. *Applied and Environmental Microbiology* 73: 5308–5319.

Carroll, G. 1988. Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. *Ecology* 69: 2–9.

Coenye, T. and P. Vandamme. 2003. Diversity and significance of *Burkholderia* species occupying diverse ecological niches. *Environmental Microbiology* 5: 719–729.

Cole, L. K., M. S. Blum, and R. W. Roncadori.. Antifungal properties of the insect alarm pheromones, citral, 2-heptanone, and 4-methyl-3-heptanone. *Mycologia*, 67: 701–708.

Compant, S., B. Duffy, J. Nowak, C. Clément, and E. A. Barka. 2005a. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Applied Environmental Microbiology* 71: 4951–4959.

———, B. Reiter, A. Sessitsch, J. Nowak, C. Clément, and E. A. Barka. 2005b. Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN. *Applied and Environmental Microbiology* 71: 1685–1693.

Cook, S. C. 2008. *Functional and Nutritional Biology of Exudate-Feeding Ants*. Ph.D Thesis, University of Utah Press.

Currie, C. R. 2001. Prevalence and impact of a virulent parasite on a tripartite mutualism. *Oecologia* 128: 99–106.

——— and A. E. Stuart. 2001. Weeding and grooming of pathogens in agriculture by ants. *Proceedings of the Royal Society of London, Series B* 268: 1033–1039.

———, A. N. M. Bot, and J. J. Boomsma. 2003a. Experimental evidence of a tripartite mutualism: bacteria protect ant fungal gardens from specialized parasites. *Oikos* 101: 91–102.

———, A. N. M. Bot, and J. J. Boomsma. 2003b. Experimental evidence of a tripartite mutualism: bacteria protect ant fungus gardens from specialized parasites. *Oikos* 101: 91–102.

———, U. G. Mueller, and D. Malloch. 1999a. The agricultural pathology of ant fungus gardens. *Proceedings of the National Academy of Sciences, USA* 96: 7998–8002.

———, J. A. Scott, R. C. Summerbell, and D. Malloch. 1999b. Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. *Nature* 398: 701–704.

———, B. Wong, A. E. Stuart, T. R. Schultz, S. A. Rehner, U. G. Mueller, G. H. Sung, J. W. Spatafora, and N. A. Straus. 2003. Ancient tripartite co-evolution in the attine ant–microbe symbiosis. *Science* 299: 386–388.

Davidson, D. W. 2005. Ecological stoichiometry of ants in a New World rain forest. *Oecologia* 142: 221–231.

———, S. C. Cook, and R. R. Snelling. 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. *Oecologia* 139: 255–266.

——— and D. McKey. 1993. The evolutionary ecology of symbiotic ant-plant relationships. *Journal of Hymenoptera Research* 2: 13–83.

———, J-P. Lessard, C. R. Bernau, and S. C. Cook. 2007. The tropical ant mosaic in a primary Bornean rain forest. *Biotropica* 39: 468–475.

do Nascimento, R. R., E. Schoeters, E. D. Morgan, J. Billen, and D. J. Stradling. 1996. Chemistry of metapleural gland secretions of three attine ants, *Atta sexdens rubropilosa*, *Atta cephalotes*, and *Acromyrmex octospinosus* (Hymenoptera: Formicidae). *Journal of Chemical Ecology* 22: 987–1000.

Emery, C. 1925. Hymenoptera fam. Formicidae, subfam. Formicinae (No. 183). In: P. Wytsman, ed. *Genera Insectorum*, Louis Desmet-Verteneuil, Brussels, 302 pp.

Fernández-Marín, H., J. K. Zimmerman, S. A. Rehner, and W. T. Wcislo. 2006. Active use of the metapleural glands by ants in controlling fungal infection. *Proceedings of the Royal Society of London, Series B* 273: 1689–1695.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biological Reviews* 63: 433–462.

GeneCodes. 2005. Sequencher 4.5 for Windows. GeneCodes Corporation, Ann Arbor, MI

Gerardo, N. M. and E. J. Caldera. 2007. Labile associations between fungus-growing ant cultivars and their garden pathogens. *The ISME Journal* 1: 373–384.

———, U. G. Mueller, and C. R. Currie. 2006. Complex host–pathogen coevolution in the *Apterostigma* fungus-growing ant–microbe symbiosis. *Evolutionary Biology* 6: 88–97.

Gilbert, G. S. and C. O. Webb. 2007. Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences* 104: 4979–4983.

Gomes De Siqueira, C., M. Bacci, Jr., F. C. Pagnocca, O. Correa Bueno, and M. J. A. Hebling. 1998. Metabolism of plant polysaccharides by *Leucoagaricus gongylophorus*, the symbiotic fungus of the leaf-cutting ant *Atta sexdens* L. *Applied Environmental Microbiology* 64: 4820–4822.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3: 193–232.

Hansen, L. D., W. J. Spangenberg, and M. M. Gaver. 1999. The infrabuccal chamber of *Camponotus modoc* (Hymenoptera: Formicidae): ingestion, digestion, and survey of bacteria. In: W. H. Robinson, F. Rettich, and G. W. Rambo, eds. *Proceedings of the 3rd International Conference on Pests*, pp. 211–219.

Harman, G. E., C. H. Howell, A. Viterbo, I. Chet, and M. Lorito. 2004. *Trichoderma* species – opportunistic, avirulent plant symbionts. *Nature Reviews* 2: 43–56.

——— and C. P. Kubicek. 1998. *Trichoderma and Gliocladium, Vol 2, Enzymes, Biological Control and Commercial Applications*. Taylor and Francis, London. 393 pp.

Hart, A. G. and F. L. W. Ratnieks. 2001. Task partitioning, division of labour and nest compartmentalisation collectively isolate hazardous waste in the leaf cutting ant *Atta cephalotes*. *Behavioral Ecology and Sociobiology* 49: 387–392.

Hölldobler, B. and H. Engel-Siegel. 1984. On the metapleural gland of ants. *Psyche* 91: 201–224.

——— and E. O. Wilson. 1990. *The Ants*. Belknap Press, Cambridge, MA. 732 pp.

Howell, C. R. 2003. Mechanisms employed by *Trichoderma* species in the biological control of plant diseases: the history and evolution of current concepts. *Plant Disease* 87: 4–10.

Hughes, W. O. H., J. Eilenberg, and J. J. Boomsma. 2002. Trade-offs in group living: transmission and disease resistance in leaf-cutting ants. *Proceedings of the Royal Society, Series B* 269: 1811–1819.

Humar, M., M. Petrič, and F. Pohleven. 2001. Changes of the pH value of impregnated wood during exposure to wood-rotting fungi. *Holz als Roh-und Werkstoff* 59: 288–293.

Jones, T. H., S. R. Brunner, A. Edwards, D. W. Davidson, and R. R. Snelling. 2005. 6-alkylsalicylic acids from *Crematogaster* cf. *difformis*. *Journal of Chemical Ecology* 31: 407–417.

———, D. A. Clark, A. Edwards, D. W. Davidson, T. F. Spande, and R. R. Snelling. 2004. The chemistry of exploding ants, *Camponotus* spp. (*cylindricus* complex). *Journal of Chemical Ecology* 30: 1479–1492.

Kaltenpoth, M. 2007. Life within insect antennae: symbiotic bacteria protect wasp larvae against fungal infestation. *Comparative Biochemistry and Physiology* 146: S66–67.

Karetnikova, E. A. and A. D. Zhirkova. 2005. Degradation of phenols formed during lignin

pyrolysis by microfungi of genera *Trichoderma* and *Penicillium*. *Biology Bulletin* 32: 445–449.

Kopper, B. J., B. L. Illman, P. J. Kersten, K. D. Klepzig, and K. F. Raffa. 2005. Effects of diterpene acids on components of a conifer bark beetle-fungal interaction: tolerance by *Ips pini* and sensitivity by its associate *Ophiostoma ips*. *Environmental Entomology* 34: 486–493.

Kredics, L., Z. Antal, L. Manczinger, A. Szekeres, F. Kevei, and E. Nagy. 2003. Influence of environmental parameters on *Trichoderma* strains with biocontrol potential. *Food Technology and Biotechnology* 41: 37–42.

Kubicek, C. P. and G. E. Harman. 1998. *Trichoderma and Gliocladium. Vol. 1. Basic Biology, Taxonomy and Genetics*. Taylor and Francis, London. 278 pp.

Little, A. E. and C. R. Currie. 2007. Symbiotic complexity: discovery of a fifth symbiont in the attine ant-microbe symbiosis. *Biology Letters* 3: 501–504.

——— and C. R. Currie. 2008. Black yeast symbionts compromise the efficiency of antibiotic defenses in fungus-growing ants. *Ecology* 89: 1216–1222.

———, T. Murakami, U. G. Mueller, and C. R. Currie. 2006. Defending against parasites: fungus-growing ants combine specialized behaviours and microbial symbionts to protect their fungus gardens. *Biology Letters* 2: 12–16.

Mackintosh, J. A., J. E. Trimble, M. K. Jones, P. H. Karuso, A. J. Beattie, and D. A. Veal. 1995. Antimicrobial mode of action of secretions from the metapleural gland of *Myrmecia gulosa* (Australian bull ants). *Canadian Journal of Microbiology* 41: 136–144.

Martínez-Aguilar, L., R. Díaz, J. J. Peña-Cabriales, P. Estrada-de los Santos, M. F. Dunn, and J. Caballero-Mellado. 2008. Multichromosomal genome structure and confirmation of diazotrophy in novel plant-associated *Burkholderia* species. *Applied and Environmental Microbiology* 74: 4574–4579.

Maschwitz, U. 1974. Vergleichende Untersuchungen zur Funktion der Ameisenmetathorakaldrüse. *Oecologia* 16: 303–310.

———, K. Koob, and H. Schildknecht. 1970. Ein Beitrag zur Funktion der Metathoracaldrüse der Ameisen. *Journal of Insect Physilogy* 16: 387–404.

Mueller, U. G., N. M. Gerardo, D. K. Aanen, D. L. Six, and T. R. Schultz. 2005. The evolution of agriculture in insects. *Annual Review of Ecology and Systematics* 36: 563–569.

Ortius-Lechner, D., R. Maile, E. D. Morgan, and J. J. Boomsma. 2000. Metapleural gland secretion of the leaf-cutter ant *Acromyrmex*. *Journal of Chemical Ecology* 26: 1667–1683.

Poulsen, M., A. N. M. Bot, C. R. Currie, and J. J. Boomsma. 2002. Mutualistic bacteria and a possible trade-off between alternative defence mechanisms in *Acromyrmex* leafcutting ants. *Insectes Sociaux* 49: 15–19.

———, A. N. M. Bot, C. R. Currie, M. G. Nielsen, and J. J. Boomsma. 2003. Within colony transmission and the cost of a mutualistic bacterium in the leaf-cutting ant *Acromyrmex octospinosis*. *Functional Ecology* 17: 260–269.

———, M. Cafaro, J. J. Boomsma, and C. R. Currie. 2005. Specificity of the mutualistic association between actinomycete bacteria and two sympatric species of *Acromyrmex* leaf-cutting ants. *Molecular Ecology* 14: 3597–3604.

Redman, R. S., D. D. Dunigan, and R. J. Rodriguez. 2001. Fungal symbiosis: from mutualism to parasitism, who controls the outcome, host or invader? *New Phytologist* 151: 705–716.

Reis, V. M., P. Estrada-de los Santos, S. Tenorio-Salgado, J. Vogel, M. Stoffels, S. Guyon, P. Mavingui, V. L. D. Baldani, M. Schmid, J. I. Baldani, J. Balandreau, A. Hartmann, and J. Caballero-Mellado. 2004. *Burkholderia tropica* sp. nov., a novel nitrogen-fixing, plant-associated bacterium. *International Journal of Systematic and Evolutionary Microbiology* 54: 2155–2162.

Rodrigues, A., M. Bacci Jr., U. G. Mueller, A. Ortiz, and F. C. Pagnocca. 2008. Microfungal "weeds" in the leafcutter ant symbiosis. *Microbial Ecology* 56: 604–614.

Rogerson, C. T. and S. L. Stephenson. 1993. Myxomyceticolous fungi. *Mycologia* 85: 456–469.

Sánchez-Peña, S. R. 2005. New view on origin of attine ant-fungus mutualism: exploitation of a preexisisting insect-fungus symbiosis (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 98: 151–164.

Santos, A. V., R. J. Dillon, V. M. Dillon, S. E. Reynolds, and R. I. Samuels. 2004. Occurrence of the antibiotic producing bacterium *Burkholderia* sp. in colonies of the leaf-cutting ant *Atta sexdens rubropilosa*. *FEMS Microbiology Letters* 239: 319–323.

SAS Institute. 2001. JMP Version 4.0.4. SAS Institute, Carey, NC

Schiøtt, M., H. H. De Fine Licht, L. Lange, and J. J. Boomsma. 2008. Towards a molecular understanding of symbiont function: identification of a fungal gene for the degradation of xylan in the fungus gardens of leaf-cutting ants. *BMC Microbiology* 8: 40.

Schulz. B., A. K. Rommert, U. Dammann, H. J. Aust, and D. Strack. 1999. The endophyte-host interaction: a balanced antagonism? *Mycological Research* 103: 1275–1283.

Shields, M. S., M. J. Reagin, R. R. Gerger, R. Campbell, and C. Somerville. 1995. TOM, a new aromatic degradative plasmid from *Burkholderia* (*Pseudomonas*) *cepacia* G4. *Applied Environmental Microbiology* 61: 1352–1356.

Shigo, A. L. 1989. *A New Tree Biology*, Ed. 2. Shigo and Trees, Associates, Durham, NH. 618 pp.

Shykoff, J. A. and P. Schmid-Hempel. 1991. Parasites and the advantage of genetic variability within social insect colonies. *Proceedings of the Royal Society of London B* 243: 55–58.

Van Borm, S., A. Buschinger, J. J. Boomsma, and J. Billen. 2002. *Tetraponera* ants have gut-symbionts related to nitrogen-fixing symbionts. *Proceedings of the Royal Society of London B* 269: 2023–2027.

van Loon, L. C., P. A. H. M. Bakker, and C. M. J. Pieterse. 1998. Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology* 36: 453–483.

Wang, Z., P. R. Johnston, Z. L. Yang, and J. P. Townsend. 2009. Evolution of reproductive morphology in leaf endophytes. *PLoS ONE* 4: e4246.

Wurdack, K. J., P. Hoffmann, R. Samuel, A. De Bruijn, M. van der Bank, and M. W. Chase. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae *sensus lato*) using plastid RBCL DNA sequences. *American Journal of Botany* 91: 1882–1900.

Zhang, M. M., M. Poulsen, and C. R. Currie. 2007. Symbiont recognition of mutualistic bacteria by *Acromyrmex* leaf-cutting ants. *ISME Journal* 1: 313–320.

J. HYM. RES.
Vol. 18(2), 2009, pp. 361–367

Venom and Task Specialization in *Termitopone commutata* (Hymenoptera: Formicidae)

JUSTIN O. SCHMIDT AND WILLIAM L. OVERAL

(JOS) Southwestern Biological Institute, 1961 W. Brichta Dr., Tucson, AZ 85745, USA; email: ponerine@dakotacom.net
(WLO) Zoology Department, Museu Paraense Emílio Goeldi, Caixa Postal 399, Belém, Pará, Brazil; email: overal@museu-goeldi.br

Abstract.—*Termitopone commutata* is a large ponerine ant species specializing in termite prey. They form raiding armies of workers that overwhelm the termite defenses, sting and inactivate termites including soldiers, and carry them back to their colony. Little natural history has been reported for this species and nothing is known of task specialization of workers. We excavated and totally censused a record-sized colony and separated individuals into categories of raiders, nest defenders, and nest workers. The amount of venom per worker in the three behavioral castes and in alate females was measured and the respective lethalities and paralyzing abilities of their venoms determined. Venom activities mirrored the needs of the three task specialists indicating matching physiology and behavior in this species.

Key words.—*Termitopone, commutata, Neoponera,* venom, paralysis, lethality

Termitopone is a small Neotropical genus of ponerine ants that are obligate specialist predators of termites (Wheeler 1936). *Termitopone commutata* (Roger) is, as Roy Snelling would say, a "handsome beast", striking not only for the enormous 15–19 mm size of the workers, but also for its smooth and shiny black sleek appearance. Although the largest of the three species in the genus, *T. commutata* also is the most poorly known. A note on taxonomy is appropriate here. The genus has been variously identified (among others) as *Neoponera, Termitopone,* and *Pachycondyla.* Recently the genus was again placed in the paraphyletic "trash" genus *Pachycondyla,* apparently as a holding position until more definitive placement could be made. For clearer communication, I will use the name *Termitopone,* though the genus likely will be placed in a newly erected *Neoponera* soon (Chris Schmidt, personal communication).

Termitopone commutata appears to be an obligate predator of any *Syntermes* spp., which they capture by stinging and paralyzing both workers and soldiers. When a scout discovers a *Syntermes* foraging group, she lays a pheromone trail back to the nest and recruits a raiding party. A raiding column then follows the attacker to the termites where the individual ants spread out and quickly attack and paralyze the termites. Upon completion of the attack, the termites are carried back to the nest (Hermann 1968; Mill 1982, 1984). Raiding columns are reported to contain about 43 ants (20–117) and travel up to 40 m (Mill 1984). Colony populations are considered small compared to the congeneric *T. marginata* (Leal and Oliveira 1995), though no colony excavations and counts have been reported. Mill (1982) estimated one observed colony to contain 400 workers.

Workers of *T. commutata* are well-known to defend their colonies vigorously and their stings have gained some notoriety for being very painful. This algogenicity of their stings has earned them roles in human social rituals, most notably in

initiation rites of girls into womanhood among Tupi-Guarani and other peoples in Amazonia (Balee 2000). Though painful, *T. commutata* stings pale in comparison to those of *Paraponera clavata*, a species not used in female rites, but reserved among some tribes for manhood rites (Balee 2000).

The dual roles of venom in *Termitopone commutata* for both prey capture and for defense against large predators makes the species an ideal model for testing the role of venom physiology in behavior. These two venom roles contrast dramatically: for prey capture, the venom is required to paralyze quickly the prey; for defense, the venom should cause immediate pain and be toxic. We report here an investigation to determine the relationship between venom physiology and individual worker behavior relative to prey capture and to defense.

MATERIALS AND METHODS

Field investigation of *Termitopone commutata* (Roger) were conducted at the Embrapa Experimental Station, Moju, Pará, Brazil 48.768890 W 1.883890 S 16 m elevation on 27–31 December 2007. The area is undisturbed older secondary growth rain forest. A column of ants was followed to a colony of *Syntermes* sp. which was raided, after which the workers carrying paralyzed termites were followed back to their nest. A sample of 19 ants was obtained from the outward bound raiding column for venom analysis. The following day all individuals in the colony were sampled and colony individuals categorized as: *raiders*, workers taken from the raiding column; *defenders*, workers that vigorously rushed out of the nest when disturbed and attempted to sting the investigators; *nest workers*, workers that retreated when the colony was being excavated and made no attempt to defend the colony; *alate females*; and *males*. Larvae, pupae, and eggs were also recorded. Live ants were frozen and maintained at ca. −6°C for up to three days during which time they were dissected to obtain venom. Pure venom was obtained from the frozen ants by the method of Schmidt (1995). In brief, frozen ants were thawed, their sting apparatuses removed to a spot of distilled water, the venom reservoir (minus filamentous glands) was pinched off and removed from the rest of the sting apparatus, rinsed with distilled water, and placed in clean distilled water. When about 50 individual reservoirs had been pooled in a single water drop, the venom was squeezed with pairs of forceps from each torn reservoir, the venom was dried over molecular sieve 5A (Supelco, Bellefonte, PA, USA) and stored in a freezer until used.

American cockroaches (*Periplaneta americana*) were used to determine the paralyzing ability were venom. Swiss white mice were used for venom lethality analyses. Venom was dissolved in cockroach ringers modified from Weidler and Sieck (1977) and 1–4 µl was injected with a 5 µl microsyringe (SGE Analytical Science, Ringwood, Victoria, Australia) through the mesocoxal-sternal membrane into groups of 6 cockroaches for worker ants and 4 cockroaches for alates. Paralysis, defined as the inability of the cockroach to move any legs, was recorded at 2 and 24 h. Cockroach death was defined as cessation of contractions of the dorsal artery (heart), complete loss of ability to move any mouthparts or the antennae, and the body turning brown. For lethality to mice, 0.15 M saline in volumes of 0.6% of the mouse body weight were injected *i.v.* into groups of 4 mice. LD_{50} values (24 hr) were calculated according to the method of Reed and Muensch (1938), with 95% confidence intervals (CI) determined by the method of Pizzi (1950), and means compared as in Woolf (1968; Chapter 19). The total paralytic and lethal activities of the venom from single ants are expressed as paralytic capacity and lethal capacity (Schmidt 1986), calculated by dividing the weight of venom per individual ant by the paralytic ED_{50} or the LD_{50} and is expressed in terms of weight of animal that would receive a median paralytic or lethal dose of venom from the sting of one average ant.

Fig. 1. Habitat of excavated *Termitopone commutata* colony showing extent of shallow nest tunnels and chambers delineated by grey sand (jar contains nest workers).

RESULTS

An outward bound raiding column approximately 5 m long and near the middle with 2–3 individuals abreast of *Termitopone commutata* was observed 16:15 local time. The column was followed to a colony of *Syntermes* sp. which was immediately raided. Within 10 minutes the raiding was essentially complete and the raiders returned to their colony carrying immobilized termites. In both the outward bound and return raiding party all individuals were moving in the same direction. The termite colony was located 82 m from the *Termitopone* colony.

The *T. commutata* nest had one main entrance with a tumulus 3 cm high and 15 cm in diameter, with several other entrances not surrounded by soil. Heavy daily rains likely washed away soil excavated from the colony, thus eliminating most of the obvious signs of nest entrances. The nest encompassed an area approximately 1.5 × 1.75 m to a depth of 20 cm (Fig. 1). Numerous chambers, mostly at a depth of 15–20 cm were found throughout the nest. The total colony census, including the few workers that returned from the field over the next two days, is listed in Table 1. No eggs were found in the colony and relatively few larvae and pupae were

Table 1. Population of *Termitopone commutata* colony.

Individual category	n
Total workers	880
Alate ♀♀	85
♂♂	4
Queen(s)	1
Pupae	14
Larvae	43
Total adult population	970

Table 2. Worker caste specialization.

Worker caste specialization	n	% of population
(Raiders, estimate	100–150	11–17)[1]
Defenders + Raiders	308	35
Nest workers	572	65
Total worker population	880	100

[1] Visual estimate of raiding column size; raiders also considered defenders

present. Few males were in the nest. In contrast, alate females numbered almost a tenth as many as the workers. Only one obvious queen was present, though others might not have been recognized, as some alate females had shed their wings and egg laying had apparently ceased.

When the colony was disturbed, defending workers "boiled" from entrances and attacked investigators. These defenders were remarkably quick, agile, and readily stung. They maintained excellent grip on the skin and were hard to shake off. Stings were almost instant, rather painful and sharp, but not "burning" like honey bee or social wasp stings, produced little flare (redness surrounding the sting site) or wheal (white area immediately around sting entry site), and the pain lasted about 3–5 minutes (n = 5 stings between two investigators). An alate female that was picked up stung the first author and produced a reaction and pain about equal to that of a worker.

A large proportion of the colony workers actively attacked when the nest was disturbed. Of 880 workers, 308 actively attacked. The remainder of the population made no attempt to attack and quickly fled when uncovered. These nest workers would attempt to sting in personal defense, but would not defend the colony as a whole. Defenders could not be distinguished from the previous day's raiders, who were presumed to become defenders when the nest was threatened. For this reason the count of raiders in Table 2 is an estimate based upon the raiding column length and density of individuals.

Venom activity.—The quantity of venom present among the female ant castes varied with both reproductive and behavioral caste. Raiders leaving the colony contained nearly twice as much venom as defenders (Table 3). Defenders, in turn, contained about 50 percent more venom than nest workers, and nest workers, in turn, contained almost twice the venom of alate females. These differences in venom quantity were obvious during the dissection process. The venom reservoirs of foragers were invariably round, full and turgid. Reservoirs of defenders varied from being half full to full (11 half full, 250 > half full). Venom reservoirs of many nest workers were collapsed and mostly empty, with a much smaller proportion being more than half full (199 mostly empty, 43 one quarter to half full, and 237 > half full). The degree of reservoir filling appeared connected to age of the worker. Many of the nest workers with mostly empty reservoirs were teneral and lighter in color, and most of the rest had clearly much softer integuments than defenders or raiders. The venom reservoirs of alate females appeared different from workers. Despite the alates being much larger than workers, their reservoirs appeared smaller in diameter

Table 3. Lethality and lethal capacity (LC) of *Termitopone commutata* venoms to mice.

Caste, or worker caste specialization	µg Venom per ant (n)	LD_{50} (µg/g)[1]	95% Conf. Interval	LC (g/sting)[1]	Rel. LC
Raiders	608 (14)	10.1	4.5–22	60.2	11.67
Defenders	366 (57)	11.3	5.4–24	32.4 **	6.28
Nest workers	237 (479)	11.3	5.7–23	21.0 ***	4.07
Alate ♀♀	131 (59)	25.4*	11–57	5.16 ****	1

[1] Probability of value different from raiders: * = <.025, ** = <.01. *** = <.001, **** = <<.001 (c-test of means, Woolf 1968).

Table 4. Paralyzing activity and paralytic capacity (PC) of *Termitopone commutata* venoms to cockroaches.

Caste, or worker caste specialization	$ED_{50,\ 2\ h}$ (μg/g)[1]	$ED_{50,\ 24\ h}$ (μg/g)[1]	$LD_{50,\ 24\ h}$ (μg/g)[1]	PC, 2 h (g/sting)	Prob different from:[1]		
					Raid	Defend	Nest W.
Raiders	61.7	113	160	9.85	-	-	-
Defenders	89.1	124	160	4.11	<.025		-
Nest workers	103	120	280	2.30	<.001	<.2	-
Alate ♀♀	113	113	160	1.16	<<.001	<.001	<.1

[1] c-test of means, Woolf 1968.

than those of workers (9 mostly empty, 37 one quarter to half full, 13 full). Moreover, unlike the clear and transparent venoms of workers, alate venom appeared turbid and contained copious quantities of flocculent particles that did not readily dissolve in water.

The defensive value against large vertebrate potential predators of the venoms of *T. commutata* can be measured in terms of lethality (LD_{50}) and lethal capacity (LC) to mice. All three behavioral castes of workers exhibited essentially the same lethality, and all are significantly more lethal than alate female venom. Among the workers, significant differences in the potential "killing" power of the venom from a single ant, or lethal capacity, became apparent. The lethal capacities of the four venoms span an 11-fold activity range between raiders and alate females, with in between values for defenders and nest workers (Table 3).

The ability of *T. commutata* to capture prey by stinging and injecting venom is measured as the effective dose for paralysis of half of the stung population (ED_{50}) at 2 h or at 24 h. Although the ED_{50} values at 2 h exhibited decreasing activities in a progression of raiders through defenders and nest workers to alate females, the differences were not significant. Some of the envenomed cockroaches recovered movement between 2 and 24 hours, as reflected in the higher amounts of venom required to maintain paralysis for 24 h compared to 2 h (Table 4). Even higher venom quantities were required to cause death in 24 h. As in defense, a stronger measure of the paralyzing ability of an individual ant is the paralytic capacity (PC). Raiders have a significantly greater ability to paralyze prey than defenders, nest workers, or alate females. Defenders are not significantly better at paralyzing prey than nest workers, but are better than alate females (Table 4).

DISCUSSION

The colony of *Termitopone commutata* investigated in this report was the largest on report, containing nearly a thousand adults. Although *T. commutata* colonies likely will be less populous than its sister species *T. marginata*, colony biomass likely equals or exceeds that of its smaller relative. The colony life cycle and periods of brood rearing and alate production are not known for *T. commutata*. Based on the absence of eggs and the small number of larvae and pupae, the present colony appeared to have just completed a production cycle of worker and reproductive rearing. If other colonies follow this pattern is not known. Wheeler (1936) commented that males of this species were unknown and subsequent papers rarely mentioned males. The colony we excavated followed this pattern of producing few males relative to alate females (4 compared to 85), a feature that could be a result of individual colony variation, loss of males from recent mating flights, or simply that males are infrequently produced. Mill's observation in June of a colony containing approximately 75 males, 400 workers, and no alate females is consistent with large colony variation in the resources devoted to male

versus female reproductive production (Mill 1982). It also suggests that *T. commutata* might have brood rearing cycles and that our colony was at the end of a brood cycle, something also supported by the large proportion of teneral workers in the colony. The presence of large numbers of alate females in our colony suggests that the low male number was not the result of recent mating flights.

Raiding behavior and defensive behavior are readily distinguished from nest activities in workers of *Termitopone commutata*. Both tasks appear to be performed by specialist workers, not simply by random workers. Behavioral task specialization is a familiar topic in sociobiology and the genetic, hormonal and molecular bases of task specialization are becoming known (Robinson et al. 2008). Examination of the actual suitability of individuals to perform certain tasks has received little attention. For termite raiding and nest defense, the ability of *T. commutata* workers to perform the tasks optimally is dependent upon venom activity and quantity. Alate females, which neither defend the colony nor raid termites, possess venom significantly less lethal and less paralytic than workers. They also produce less venom than workers. This pattern is consistent with those of other species where reproductive and worker venoms have been compared (Schmidt and Schmidt 1985) and makes sense in terms both of resource allocation and behavioral needs.

Worker *T. commutata* behavioral castes contain different amounts of venom in their reservoirs, with raiders having the greatest amount, and nest workers the least. Unfortunately, the necessity to pool venom from many individuals to make the weight measurements precludes ability to test for significant differences among the groups. Both the lethalities and paralyzing abilities of the venoms of the worker castes were similar, if not, identical. This finding suggests that venom composition and synthesis do not change with either age or behavior of the individual, rather that venom production varies with age and, perhaps, with task specialization. The affect of venom production on ability of workers to perform raiding and defensive tasks is clearly seen in the measures of paralytic and lethal capacities. In both cases raiders or defenders have significantly greater ability to paralyze prey and to damage potential predators than nest workers. Thus, those workers that are physiologically best adapted for performing the tasks of prey capture and defense are those workers that actually perform the tasks, and those workers less able do not put themselves at risk performing tasks for which they are ill suited.

ACKNOWLEDGMENTS

This paper is dedicated to Roy Snelling who has been a great mentor to numerous young scientists and who has been a wonderful and enjoyable colleague to many of us. My career of studying venoms and aculeate Hymenoptera was started, in part, by Roy who collected *Pogonomyrmex* ants and transported them alive for me (JOS) to Georgia in his tiny MG car. To Roy, for his witty remarks and his camaraderie, a hearty thanks.

Thanks also to Krista Schmidt who assisted in colony excavation.

LITERATURE CITED

Balee, W. 2000. Antiquity of traditional ethnobiological knowledge in Amazonia: the Tupi-Guarani family and time. *Ethnohistory* 47: 399–422.

Hermann, H. R. Jr. 1968. Group raiding in *Termitopone commutata* (Roger) (Hymenoptera: Formicidae). *Journal of the Georgia Entomological Society* 3: 23–24.

Leal, I. R. and P. S. Oliveira. 1995. Behavioral ecology of the Neotropical termite-hunting ant *Pachycondyla* (=*Termitopone*) *marginata*: colony founding, group-raiding and migratory patterns. *Behavioral Ecology and Sociobiology* 37: 373–83.

Mill, A. E. 1982. Emigration of a colony of the giant termite hunter *Pachycondyla commutata* (Roger) (Hymenoptera: Formicidae). *Entomologists Monthly Magazine* 118: 243–45.

———. 1984. Predation by the ponerine ant *Pachycondyla commutata* on termites of the genus *Syntermes* in Amazonian rain forest. *Journal of Natural History* 18: 405–10.

Pizzi, M. 1950. Sampling variation of the fifty per cent end-point, determined by the Reed-Muench (Behrens) method. *Human Biology* 22: 151–190.

Reed, L. J. and H. Muench. 1938. A simple method of estimating fifty per cent endpoints. *American Journal of Hygiene* 27: 493–497.

Robinson, G. E., R. D. Fernald, and D. F. Clayton. 2008. Genes and social behavior. *Science* 322: 896–900.

Schmidt, J. O. 1986. Chemistry, pharmacology and chemical ecology of ant venoms. Pp. 425–508 *in*: Piek, T., ed. *Venoms of the Hymenoptera*. Academic Press, London. 570 pp.

———. 1995. Toxicology of venoms from the honeybee genus *Apis*. *Toxicon* 33: 917–927.

Schmidt, P. J. and J. O. Schmidt. 1985. Queen versus worker venoms: are they equally lethal? *Toxicon* 23: 38–39.

Weidler, D. J. and G. C. Sieck. 1977. A study of ion binding in the hemolymph of *Periplaneta americana*. *Comparative Biochemistry and Physiology* 56A: 11–14.

Wheeler, W. M. 1936. Ecological relations of ponerine and other ants to termites. *Proceedings of the American Academy of Arts and Sciences* 71: 159–243.

Woolf, C. M. 1968. *Principles of Biometry, Statistics for Biologists*. Van Nostrand, Princeton, New Jersey. 359 pp.

J. HYM. RES.
Vol. 18(2), 2009, pp. 368–379

Urban Bee Diversity in a Small Residential Garden in Northern California

GORDON W. FRANKIE, ROBBIN W. THORP, JAIME C. PAWELEK, JENNIFER HERNANDEZ AND ROLLIN COVILLE

(GWF, JCP, RC) College of Natural Resources, University of California, Berkeley, California 94720
(RWT) Department of Entomology, University of California, Davis, California 95616
(RC) Private entomological consultant, bee biologist, nature photographer

Abstract.—Bee species diversity is known to be high in numerous urban areas worldwide. In California our research group from the University of California at Berkeley and Davis has been conducting surveys statewide of urban bee species and their preferred host plant flowers since 2005 and find that many cities also have high species diversity. In this paper we examine in some detail the bee-flower relationships in one small residential garden in northwestern California – Ukiah in Mendocino Co. In this garden, which is densely packed with preferred bee plants, we have recorded 68 bee species; citywide, Ukiah has 91 recorded species. High bee diversity in the garden is believed to be related to the high diversity and abundance of plant materials that provide a continuous source of pollen and nectar during the entire growing season. Bee visitation counts on selective (target) plant types indicate the bee-flower relationships are relatively predictable, and this information can be used to plan and establish bee habitat gardens.

Studies on diversity of bee species in urban environments worldwide have been increasing in recent years (see reviews in Cane 2005; Hernandez et al. 2009b). Some of these studies have undoubtedly resulted from research to document more of Earth's biodiversity, even in environments that have been severely disturbed by human activities and development. Increasing also are popular and semi-technical publications that provide objective biological profiles on the wide variety of organisms that live with us in the ever-expanding city environments (Grissell 2001; Lowry 1999, 2007; Tallamy 2009). In an earlier and relevant volume, Owen (1991) produced an extraordinary account of 15 sequential years of documenting the biodiverse organisms that came to visit her small residential garden in Leceister England. She also points out the significance of gardens for conserving wildlife. Thus, there is a definite new trend or movement towards recognizing interesting and desirable urban fauna and how to encourage and enjoy these organisms that frequent and establish in our gardens (Hayes 2003; Carroll and Salt 2004; Stone and Barlow 2005; Louv 2008; Tallamy 2009; Frankie et al. 2009).

The University of California at Berkeley and Davis have been surveying urban bees in California since the late 1990s with the general goal of increasing knowledge about a group of common insects that have established ecological relationships with gardens and have gone largely unnoticed, until recently, when the value of all bees became better known through Colony Collapse Disorder (CCD) of our important honey bees (NRC 2007). Since 2005 our research group has focused on a statewide survey of urban bee diversity and ecology, especially with regard to preferred ornamental host flowers. The first paper on this work (Frankie et al. 2009) provides an

overview of our findings through 2007. As this work continues it is clear that urban areas can support a rich assortment of bee species if the right floral and other resources are present (Ahrne et al. 2009).

In this paper we present findings from one of the gardens in the city of Ukiah, Mendocino Co. in northwestern California where there is rich diversity of plants and native bee species. Goals of this paper are first, to examine in some detail the floral relationships of garden plants (origin, flowering season, pollen/nectar resources) to local native California bee species over the period 2005 through 2008. Second, to compare the bee findings of the study garden with bee totals for the rest of Ukiah.

Site description: Ukiah Garden.—The city of Ukiah (pop. 15,497, as of 2000; elevation ~186 m) is located in Mendocino Co. in northwestern California in a large valley surrounded by low elevation mountains (up to ~1,065 m in elevation). Most of the city is in the western half of the valley, including the study garden. The eastern half of the valley is largely agricultural with pear orchards and vineyards. Almost all houses and gardens in Ukiah can be considered residential, and in most lots land has been cleared and houses and gardens established. Because Ukiah is inland and somewhat isolated by mountains, summers are hot and dry, but with cool evenings. Winters are mild to cold with occasional periods of frost and freezing temperatures, which has limited the use of some ornamental plant materials in the area.

As in almost every California city, urban residents in Ukiah use a high percentage of non-native plant materials in their gardens (Frankie et al. 2005, 2009). In this regard, the study garden is no exception as about 75% of its ornamental plants are non-natives (Table 1). The garden is unique, however, in that it contains a relatively high diversity of plant materials compared to others surveyed throughout the city. The garden was first planted in 2004, and selection of ornamental plants was based on the organic garden at the Fetzer winery in nearby Hopland (~16 km SSE of Ukiah). Fortuitously, most of the selected plant types are attractive to local bees.

The Ukiah garden was like most gardens in urban California, that is, dynamic with some plants progressively added and others removed over the period 2005-present. Most plant types were perennial and planted on a thick layer of topsoil that was originally brought to the garden in 2004. The closest natural area is 400+ meters to the west where houses stop at the edge of an extensive and dense oak-woodland habitat that occurs on a steep mountain hillside. Important bee plants such as *Arbutus menziesii* Pursh and several *Arctostaphylos* and *Ceanothus* species are widely scattered in this habitat. Open grassland is rare on the hillside. Westward within a km of the study garden are a few small, scattered patches of chaparral vegetation; within two km are larger patches. About five km east of Ukiah is the Mayacmas Range of mountains that is predominated with well developed and diverse chaparral vegetation. The entire wild area around Ukiah is filled with many native wildflower species (Stearns 2007).

The main part of the Ukiah garden was south facing in the front of the house and measured ~100 m^2 (10 m × 10 m). Two pathways traversed the garden and met at a front gate. A small narrow strip of garden was located on the east side of the house, which measured ~20 m^2. The vast majority of bee plants were found in the front yard. Plants in both the front and side yards received regular watering, pruning, and weeding. In the front yard plants were packed tightly in this relatively small space (Fig. 1). Plants in the side yard were spaced more widely.

MATERIALS AND METHODS

Bee and plant survey work at the Ukiah garden was initiated during the summer of 2005; three visits were made that year. In subsequent years visits were made several

times during the entire growing season: 2006 (9 visits), 2007 (13), and 2008 (12). Bee collections and bee frequency counts were made each year.

Voucher bee species were collected with aerial nets from all garden flowers that showed attraction to bees. Collected bees were transported to the lab at UC Berkeley, curated and sent to the bee lab at UC Davis to be identified by R. Thorp. Records of identified bees are kept on file in both labs; curated bees are permanently housed at UC Berkeley.

Bee frequency counts were made on selected (target) plant types in order to track bee diversity and abundance through time (see coded plants in Table 1). Patches (~1–1.5 m square) of target plant types in good flower were observed for three-minute periods, and each bee that made contact with reproductive flower parts was counted. Once counted on the first flower visited, they were not counted again, which allowed for focus on any new bee(s) entering the patch. Numerous bee counts were made on target plants during each year when the main bloom period occurred. Some bee taxa could be identified on the flowers, whereas others had to be collected to confirm identification. Counts provided bee diversity and abundance measures that were tallied and averaged for each plant type (Frankie et al. 2005, 2009). In this paper we focus on bee diversity measures. Future papers will be concerned with abundance measures for the study garden and the entire city of Ukiah.

Most target plants chosen in this study were the same ones used in an ongoing statewide survey of urban bees and their host flowers (Frankie et al. 2009). Because several target plants were either missing or in limited numbers, we added these plants in 2007 and 2008 to record bee activity (see coded plants in Table 1). Most added plants provided useful information, but a few such as *Encelia californica* Nutt., *Salvia* 'Indigo Spires', and *Duranta erecta* L. survived only one season. These species were not adapted to the cold temperatures that occur during winter in Ukiah.

RESULTS

We recorded all plant types (55) found in the garden that showed attraction to bees over the period of 2005–2008 (Table 1). There were a very few others that did not attract bees (e.g. ornamental grass) or were non-reproductive; all of these were small in size and not recorded. As indicated in Table 1, bees were attracted to plants in 19 different families with Asteraceae and Lamiaceae having the greatest number of representative species (15 each). Members of these two families together represented almost 55% of the plant types in the garden. Frankie et al. (2005) also found plants in these two families to be the most important sources of pollen and nectar in two San Francisco Bay Area cities.

The 55 plant types listed in Table 1 consisted of 14 California natives (25%) and 41 non-natives (75%). Together they provided pollen and nectar for bees during each month of the year (Wojcik et al. 2008). Further, many of the plants have long flowering periods, some of which spanned two seasons. Examples of these included *Bidens ferulifolia* DC., *Coreopsis grandiflora* cvs, *Cosmos bipinnatus* Cav., *Erigeron glaucus* Ker Gaw., and *Solidago californica* Nutt. for pollen and nectar, and *Lavandula* sp. 2, *Nepeta* × *faassenii* Bergmans, *Perovskia atriplicifolia* Benth., *Salvia uliginosa* Benth., and *Linaria purpurea* (L.) Mill. for nectar. This resource continuity, which results in several plant types being in flower simultaneously, is believed to be one of the main factors sustaining diverse bee species during the growing season.

Bee taxa collected at the Ukiah garden from 2006 through 2008 are listed in Table 2. To date, 68 species in 26 genera and five families have been recorded, with most species in the families Megachilidae (32) and Apidae (19). Collections of bee species increased during each year (30, 40, 53

respectively), and this was related, in part, to more visits made in 2007/2008 than 2006 and to the added bee-attractive plants during the latter two years (Table 1). The overall list of bee taxa recorded from this and other Ukiah gardens for the study period was 91 species in 28 genera and five families.

Bee seasonality.—Many of the bee species had seasonal patterns of occurrence, that is, spring, summer, or both seasons (Table 2). Additional ongoing collections are considered necessary for characterizing more precisely the seasonality for most species, however, some patterns are presented here that are well known for selected genera/species in northern California.

There were several groups of spring-season bee taxa (Table 2). The most prominent groups were in the genera *Andrena* (Andrenidae) and *Osmia* (Megachilidae). The two *Andrena* species, *A. auricoma* Smith and *A. cerasifolii* Cockerell, were exclusively spring bees, and 10 of 12 recorded *Osmia* species were spring bees. One of 12 *Osmia* was a spring/early summer species; *Osmia regulina* Cockerell was a summer bee. In the Apidae, *Anthophora californica* Cresson, *Eucera frater albopilosa* (Fowler), and *Habropoda depressa* Fowler are well known spring bees. *Bombus* species (4) are primitively eusocial and thus multiple season bees, but most were in relatively high abundance during this period. Although three of four species were also collected in summer, their frequencies were substantially lower. This is probably due to the fact that two species (*B. melanopygus* Nylander and *B. vosnesenskii* Radoszkowski) start their nests in January and peak in early spring.

The most prominent group of summer bees was in the genus *Megachile* (Megachilidae). Seven of nine listed species were collected in summer. Two of the nine, *M. apicalis* Spinola and *M. rotundata* (Fabricius), which were introduced in California, were found during both seasons. Only one species, *M. lippiae* Cockerell, was collected in spring. In the Apidae, *Melissodes robustior* Cockerell was a summer bee; *M. lupina* Cresson, although rarely collected, was also a summer bee.

Numbers of plant types visited by each bee species were compiled and sorted to California natives and non-natives (Table 2). We also arbitrarily divided the bees into two groups: species that visited relatively few host plant types (1–4 natives plus non-natives), and those (5 and above) that had a wider host range. In the first group there were 54 bee species and the vast majority of them (41) were collected on only one or two hosts. The second group had 15 species, which included all four of the introduced species, *Apis mellifera* Linnaeus, *Hylaeus punctatus* (Brulle) (Colletidae), *Megachile apicalis*, and *M. rotundata*. As expected the host range of *A. mellifera* was the highest with 21 plant types visited, followed by *M. rotundata* with 12 host types. The three California native bee species with the widest host ranges were *Halictus ligatus* Say (Halictidae) (10 plant types) and two apids, *Xylocopa tabaniformis orpifex* Smith (9 types) and *Ceratina acantha* Provancher (8 types). It is noteworthy that California native bees in the second group (11 of 15 species) were collected more frequently (10 of 11 species) on non-native host plants.

Plant–bee relations.—Some plant species had an unusual capacity to attract high bee diversity. We examined this capacity in native and non-native plant types having the greatest bee diversities (Table 3). In the natives, *Carpenteria californica* Torr., *Solidago californica* and *Erigeron glaucus* had the highest bee species diversities. In non-native plants, bee species counts were higher than natives in four of five plant types. Most attractive non-natives are nectar resources in the Lamiaceae. Except for *C. californica*, which has a relatively short flowering period (May), the long blooming periods of the other nine plants (Table 3) allowed them to be exposed longer to a greater diversity of bee species. All but *C. californica* bloomed for at least three months. This phenological character-

Table 1. Plants attracting bees in the Ukiah study garden from 2005–2008. Plant names according to Hickman (1993) and Brenzel (2007). Cultivars = cvs.

Plant species or cultivars (cvs)	Plant Origin[1]	Flowering Period[2]	Floral Reward[3]
Apiaceae			
Eryngium sp.[4]	Non-Nat	Sum	N
Asteraceae			
Achillea millefolium L.[5]	Nat	Spr-Sum	N/P
Achillea 'Moonshine'	Non-Nat	Spr-Sum	N/P
Aster × *frikartii*[4,5]	Non-Nat	Sum-Fall	N/P
Bidens ferulifolia DC.[4,5]	Non-Nat	Spr-Fall	N/P
Centaurea cineraria Pall.	Non-Nat	Spr-Sum	N/P
Coreopsis grandiflora - 2 cvs[4,5]	Non-Nat	Sum	N/P
Cosmos bipinnatus Cav.[4,5]	Non-Nat	Sum-Fall	N/P
Cosmos sulphureus Cav.[4,5]	Non-Nat	Sum-Fall	N/P
Encelia californica Nutt.[4]	Nat	Spr-Fall	N/P
Erigeron glaucus 'Wayne Roderick'[4,5]	Nat	Spr-Sum	N/P
Erigeron karvinskianus DC.[5]	Non-Nat	Spr-Fall	N/P
Gaillardia × *grandiflora* Hort.[5]	Non-Nat	Spr-Fall	N/P
Grindelia hirsutula Hook. & Arn.[4]	Nat	Spr-Sum	N/P
Solidago californica Nutt.[5]	Nat	Sum-Fall	N/P
Bignoniaceae			
Campsis radicans (L.) Seem.	Non-Nat	Spr	?
Boraginaceae			
Echium wildpretii H.Pearson ex Hook.f.	Non-Nat	Spr	N/P
Brassicaceae			
Lobularia maritima Desv.	Non-Nat	Spr-Sum	N
Buddlejaceae			
Buddleja davidii Franch.	Non-Nat	Sum	N
Crassulaceae			
Sedum sp.	?Non-Nat	Sum	N
Fabaceae			
Wisteria sinensis Sweet[5]	Non-Nat	Spr	N
Iridaceae			
Sisyrinchium bellum S.Watson	Nat	Spr	N/P
Lamiaceae			
Calamintha nepetoides Jord.[4]	Non-Nat	Sum-Fall	N
Lavandula stoechas L.[5]	Non-Nat	Spr-Sum	N
Lavandula - sp. 2[5]	Non-Nat	Spr-Fall	N
Lavandula - sp. 3[5] (white flowers)	Non-Nat	Sum	N
Nepeta × *faassenii* Bergmans[5]	Non-Nat	Spr-Fall	N
Perovskia atriplicifolia Benth.[5]	Non-Nat	Sum	N
Salvia apiana Jeps.	Nat	Spr	N
Salvia brandegeei Munz	Nat	Spr	N
Salvia clevelandii (A. Gray) E. Greene *or S. leucophylla* Greene	Nat	Spr	N
Salvia greggii (2 cvs)[5]	Non-Nat	Spr-Fall	N
Salvia 'Indigo Spires'[4,5]	Non-Nat	Spr-Fall	N
Salvia uliginosa Benth.[4,5]	Non-Nat	Sum	N/P
Salvia guaranitica A.St.-Hil. ex Benth.	Non-Nat	Sum	N
Teucrium × *lucidrys* Boom (*T. chamaedrys* L.)	Non-Nat	Sum	N
Liliaceae			
Allium sp.	Non-Nat	Spr	N
Onagraceae			
Epilobium canum (Greene) P.H. Raven	Nat	Sum	N
Gaura lindheimeri Engelm. & Gray	Non-Nat	Sum	N
Philadelphaceae			
Carpenteria californica Torr.	Nat	Spr	P

Table 1. Continued.

Plant species or cultivars (cvs)	Plant Origin[1]	Flowering Period[2]	Floral Reward[3]
Plantaginaceae			
Antirrhinum majus L.	Non-Nat	Spr	?N/P
Polygonaceae			
Eriogonum grande Green var. *rubescens* Munz	Nat	Sum	N
Eriogonum umbellatum Torr.	Nat	Spr-Sum	N
Ranunculaceae			
Aquilegia sp.	Non-Nat	Spr	N
Rutaceae			
Ruta graveolens L.	Non-Nat		N
Scrophulariaceae			
Linaria purpurea (L.) Mill.[4,5]	Non-Nat	Sum-Fall	N
Penstemon digitalis 'Husker's Red'	Non-Nat	Spr	N
Penstemon 'Midnight'	Non-Nat	Spr	N
Penstemon sp. (red flower)	Non-Nat	Spr	N
Penstemon heterophyllus S.Watson[4]	Nat	Spr	N
Verbenaceae			
Aloysia triphylla Royle	Non-Nat	Sum	N
Duranta erecta L.[4]	Non-Nat	Sum	N
Verbena bonariensis L.	Non-Nat	Sum	N
Total: 55 types (includes all cultivars)			

[1] Nat- California native plant; Non-Nat- not native to California flora
[2] Spr- Spring; Sum- Summer; Fall
[3] N- Nectar; P- Pollen
[4] Plants progressively added to garden over period 2006–2008
[5] Bee frequency counts were collected on these target plants

istic coupled with their inherent attraction (Frankie et al. 2005, 2009) probably accounts for part of the higher diversity levels.

A relationship between flower patch size and bee diversity was also suggested from results presented in Table 3. It appears that large patch size of some bee-attractive plant types may attract high bee diversities. In the case of two natives, *Carpenteria californica* and *Solidago californica*, and the first four non-native plant types (Table 3), all had patches of more than 1.5 m^2 of flowering space. Frequency counts in subpatches (~1–1.5 m^2) in all but *Carpenteria californica* (Table 1) were used to determine the high bee diversities in each of these selected species. Experimental studies will be needed in the future to further examine this relationship.

Many plant types flowered simultaneously during any given time period. The seasonal bee species sort themselves among simultaneously flowering types in relatively different and predictable patterns (Frankie et al. 2009). Numerous bee frequency counts that have been gathered over three years of monitoring exemplify how summer flowering *Solidago californica*, *Erigeron glaucus*, and *Perovskia atriplicifolia* attracted different bee groups during coinciding flowering periods. In descending order of occurrence, *Solidago* attracted mostly halictids, then honey bees, non-*Osmia* megachilids, and *Ceratina* species. *Erigeron* attracted non-*Osmia* megachilids, halictids, and *Ceratina*. *Perovskia* attracted mostly honey bees, then non-*Osmia* megachilids, and *Ceratina* species (Fig. 2). *Nepeta* × *faassenii*, which flowers extensively in both seasons attracted honey bees, *Ceratina* species, and non-*Osmia* megachilids in the summer, but in spring the same *Nepeta* plants attracted somewhat different bee species and frequencies: honey bees, *Bombus* species, and *Osmia* species. Thus, on a

Fig. 1. Ukiah study garden during a spring bloom.

given summer observation day, when all four plant types are in flower, one can expect certain frequencies of bee taxa on one plant type and different sets on the other three host plant types.

Simultaneous flowering of several species had another behavioral-ecological effect that was first observed during the survey of bee-attractive plants in two San Francisco Bay Area cities from 1999–2003 (Frankie et al. 2005). Some plant species that are usually unattractive to bees such as *Achillea millefolium* L., *Erigeron karvinskianus* DC., and *Verbena bonariensis* L. become attractive when diverse and attractive flowering species surround them. Apparently, bees will try out these plants because of their close proximity to attractive plants. Once tested, these "unattractive plants" become attractive. We have observed this phenomenon previously in other surveyed California gardens, for example, in Sacramento and La Canada Flintridge (near Pasadena).

Ukiah Garden versus Greater Ukiah

Four bee taxa in the Ukiah garden were compared and contrasted with the same taxa from collections made in other gardens throughout the city of Ukiah where a total of 91 species have been recorded to date. These taxa were selected because they provide insight on host plant factors that may be responsible for the extant bee list at the Ukiah garden.

Osmia.—*Osmia* species are well represented with 12 of the 15 city species found in the garden. The most important host plants in the garden were *Lavandula* sp. 2, *Linaria purpurea*, and *Nepeta* × *faassenii*. Citywide, *Osmia* were also found on *Phacelia tanacetifolia* Benth.

Andrena.—Only two of 10 city species were found in the garden. Examination of

host records clearly indicates that *Andrena* species not found in the garden were associated with mostly California natives: *Ceanothus* species and *Arbutus menziesii*, neither of which are in the garden. One of the city *Andrena* species was found on flowers of the non-native *Philadelphus coronarius* L. (sweet mock orange). Other researchers have also noted a scarcity of *Andrena* in urban gardens (Antonini and Martins 2003; Fetridge et al. 2008).

Agapostemon texanus Cresson is one of the most common bee species found on a variety of urban host plants in California (Frankie et al. 2009), however, we have yet to collect it in the Ukiah garden. In greater Ukiah it was only collected once on chicory flowers.

Lasioglossum.—Only five species were found in the garden, yet 12 species have been collected throughout Ukiah on plants of *Ceanothus* sp., *Eschscholzia californica* Cham., *Ceanothus* 'Julia Phelps', *Convolvulus arvensis* L., and *Centaurea solstitialis* Asso. None of these plant types were in the study garden.

DISCUSSION AND CONCLUSIONS

Although the study garden had a high diversity of bee species, numbers could have been higher if more aggressive sampling methods had been used, for example pan traps (Wojcik et al. 2008; Hernandez 2009b), vane traps (R. Thorp pers. com.), and with earlier season visits (Feb./Mar.) and more frequent monitoring intervals of every two to three weeks. Further, if more host plants of other bee species were added, it would also probably increase bee species diversity. In this regard, adding *Ceanothus* shrubs or *Arctostaphylos* species to the garden would likely result in more *Andrena* species to the former and increased abundance of *Bombus* and *Anthophora* species to the latter. *Ceanothus* 'Julia Phelps' and *C.* 'Dark Star' were just added in June 2009, and two *Arctostaphylos* species in an adjacent fallowed lot to the study garden are scheduled for monitoring in early 2010. Thus, high diversity of the right plant types flowering in sequence over a growing season can result in high bee diversity in the Ukiah area.

This relationship of preferred high plant diversity to high bee diversity was also demonstrated at the University of California, Berkeley Oxford Tract where in 2003/2004 a specially constructed garden was designed to provide preferred pollen and nectar of ornamentals to local native bees for the entire growing season (Wojcik et al. 2008; Hernandez et al. 2009a). At the end of the growing season in 2004, the plants had attracted 37 bee species (Hernandez 2009a). Additional sampling since then has added seven more species to the list (R. Thorp and J. Hernandez, pers. com.). Other gardens in the state (Frankie et al. 2009) that fortuitously provide preferred bee plants during the growing season are found in Sacramento (Masonic Lawn Cemetery with 69 bee species) and La Canada Flintridge (Descanso Gardens with 94 bee species).

Most surveyed urban areas in California have diverse floral resources that diverse native bees need for reproduction and survival (Frankie et al. 2009). There are a few urban areas, however, where the right plant types for native bees are scarce, widely scattered, or nonexistent, and this pattern seems to reflect local gardening practices and plant selections (B. Ertter, UC Berkeley Jepson Herbarium, pers. com.). In these few urban areas, which include the cities of Monterey-Carmel-Pacific Grove, Paso Robles, and San Diego, preferred bee plants are scarce and widely scattered as are the native bee species (G. Frankie, unpub.).

In the case of Ukiah and other California cities, most plants used in gardens are non-natives to the state. Although native California bees coevolved with certain native plants, many have the capacity and flexibility to use a variety of plants, including some non-natives. A preliminary survey of native versus non-native bee plants in Berkeley revealed that of the 1000+ plant types used in this city, only ~50 were natives; ~950 were non-natives.

Table 2. List of bee taxa collected at Ukiah garden from 2006–2008. Numbers of California native and non-native plant types visited by each bee species are listed respectively in parens.

Bee species	2006	2007	2008	Bee Season[1]
ANDRENIDAE				
Andrena auricoma Smith (1,1)			+	Spr
Andrena cerasifolii Cockerell (1,0)			+	Spr
APIDAE				
Anthophora californica Cresson (0,1)		+	+	Spr
Anthophora urbana Cresson (0,1)	+	+	+	Spr/Sum
Apis mellifera Linnaeus[2] (5,16)	+	+	+	Spr/Sum
Bombus californicus Smith (0,1)		+		Spr
Bombus flavifrons Cresson (1,3)	+	+	+	Spr/Sum
Bombus melanopygus Nylander (1,4)		+	+	Spr/Sum
Bombus vosnesenskii Radoszkowski (0,3)	+		+	Spr/Sum
Ceratina acantha Provancher (2,6)	+	+	+	Spr/Sum
Ceratina nanula Cockerell (1,3)	+	+	+	Spr/Sum
Ceratina sequoiae Michener (0,1)		+	+	Sum
Ceratina tejonensis (1,3)	+	+	+	Spr/Sum
Eucera frater albopilosa (Fowler) (0,1)		+	+	Spr
Habropoda depressa Fowler (0,2)		+	+	Spr
Melissodes lupina Cresson (1,0)	+			Sum
Melissodes robustior Cockerell (0,6)	+	+	+	Sum
Melissodes tepida timberlakei Cockerell (1,3)	+	+	+	Spr/Sum
Nomada sp. CM (0,1)			+	Spr
Nomada sp. F (1,0)			+	Spr
Xylocopa tabaniformis orpifex Smith (1,8)	+	+	+	Spr/Sum
COLLETIDAE				
Colletes kincaidii Cockerell (1,0)			+	Sum
Hylaeus episcopalis (Cockerell) (0,1)		+		Spr
Hylaeus mesillae Cockerell (3, 6)	+	+	+	Spr/Sum
Hylaeus polifolii (Cockerell) (1,2)		+	+	Sum
Hylaeus punctatus (Brule)[2] (5,0)	+	+	+	Spr/Sum
Hylaeus verticalis (Cresson) (0,1)		+		Sum
HALICTIDAE				
Halictus farinosus Smith (2,4)	+	+	+	Spr/Sum
Halictus ligatus Say (4,6)	+	+	+	Spr/Sum
Halictus tripartitus Cockerell (3,4)	+	+	+	Spr/Sum
Lasioglossum incompletus (Crawford) (1,0)			+	Sum
Lasioglossum tegulariformis (Crawford) (1,2)			+	Spr/Sum
Lasioglossum (Dialictus) sp. F (0,1)			+	Sum
Lasioglossum (Dialictus) sp. 2 (0,1)	+			Sum
Lasioglossum (Evylaeus) sp. (1,0)	+			Sum
Sphecodes sp. CM (1,0)			+	Sum
MEGACHILIDAE				
Anthidiellum notatum robersoni (Cockerell) (0,1)	+		+	Sum
Anthidium illustre Cresson (0,1)			+	Sum
Anthidium placitum Cresson (0,1)			+	Sum
Ashmeadiella cactorum basalis Michener (0,1)		+		Sum
Ashmeadiella timberlakei solida Michener (0,1)			+	Spr
Coelioxys apacheorum Cockerell (0,1)		+		Sum
Dianthidium ulkei (Cresson) (3,2)	+		+	Sum
Dolichostelis laticincta Cresson (0,1)		+	+	Sum
Heriades occidentalis Michener (2,3)	+	+	+	Spr/Sum
Hoplitis producta gracilis (Michener) (0,1)			+	Spr
Megachile angelarum Cockerell (0,4)	+	+	+	Sum
Megachile apicalis Spinola (0,5)	+	+	+	Spr/Sum
Megachile coquilletti Cockerell (0,1)		+		Sum

Table 2. Continued.

Bee species	2006	2007	2008	Bee Season[1]
Megachile fidelis Cresson (1,5)	+	+	+	Sum
Megachile frugalis Cresson (0,3)		+	+	Sum
Megachile gentilis Cresson (1,2)	+			Sum
Megachile lippiae Cockerell (1,0)			+	Spr
Megachile montivaga Cresson (0,1)		+		Sum
Megachile rotundata (Fabricius)[2] (3,9)	+	+	+	Spr/Sum
Osmia aglaia Sandhouse (0,1)			+	Spr
Osmia calla Cockerell (0,1)		+		Spr
Osmia coloradensis Cresson (2,2)		+	+	Spr
Osmia cyanella Cockerell (1,3)	+	+	+	Spr
Osmia densa Cresson (0,1)		+		Spr
Osmia gabrielis Cockerell (0,1)			+	Spr
Osmia granulosa Cockerell (0,2)	+		+	Spr/Sum
Osmia lignaria propinqua Cresson (0,1)		+		Spr
Osmia montana Cresson (1,0)			+	Spr
Osmia nigrifrons Cresson (0,1)			+	Spr
Osmia regulina Cockerell (1,2)	+		+	Sum
Osmia sp. A (0,1)		+		Spr
Protosmia rubifloris (Cockerell) (2,2)	+		+	Spr/Sum
Species Totals:	30	40	53	
Totals for all years: 5 families, 26 genera, 68 species				

[1] Spr-spring; Sum-summer
[2] Introduced bee species in California

Further, about 80% of the natives attracted bees at measurable levels, whereas slightly less than 10% of the non-natives attracted bees. Still, this 10% amounted to ~90 attractive plant types (Frankie et al. 2005). Further, many to most bee-plant relationships in Berkeley and most other gardens in the state are relatively predictable (Frankie et al. 2009). That is, certain bee taxonomic groups can be expected to be associated with given plant types, and this predictability allows for planning of bee gardens, which are now becoming more common in California and elsewhere (Pawelek et al. 2009). Other authors have also commented on the value of using native and non-native plants for pollinator gardens (Fetridge et al. 2008).

A synthesis of findings in this study suggests that in the case of Ukiah and probably several other California cities, planning for a highly diverse bee garden will depend on several plant factors including: 1) high plant diversity of the right native and non-natives, 2) a complete seasonal sequence of bee plants that provide a continuum of pollen and nectar, and 3) probably large flowering patch sizes of the most attractive plant types. Another key factor is availability of nesting substrates. Nesting bees have only rarely been observed in the Ukiah study garden, which suggests that most species probably came from outside the garden. In a relevant paper, Cane (2005) calls attention to the three needs of bees: floral resources, nesting opportunities, and "condition of the urban matrix." In the case of the Ukiah garden, condition of the urban (or environmental) matrix becomes all-important as it appears that most bees come from the surrounding area, which probably includes nearby wild areas.

Finally, updates on the California statewide survey of urban bee species and their preferred plant types can be found at our website: http://nature.berkeley.edu/urbanbeegardens. More than 225 bee species have been collected already from the surveyed cities of Redding, Ukiah, Sacra-

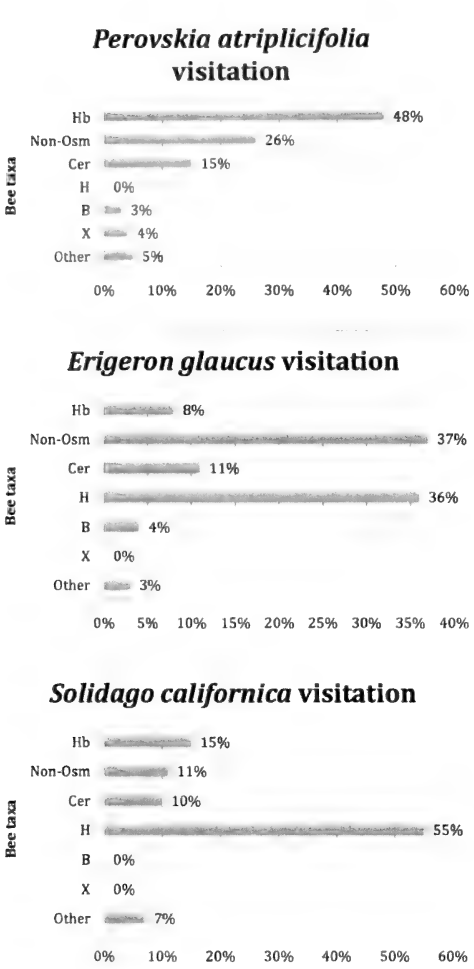


Fig. 2. Visitation percentages of main bee taxa to three host plant flowers. Percentages based on totals of bee frequency counts over study period: *Perovskia* (n= 54 counts), *Erigeron* (n= 32 counts), *Solidago* (n= 46 counts). Hb – honey bees, Non-Osm – non- *Osmia* megachilids, Cer – *Ceratina*, H – halictids, B – *Bombus*, X – *Xylocopa*, Other – bee taxa at lower % levels.

mento, Berkeley, and Santa Cruz in northern California, and San Luis Obispo, Santa Barbara, La Canada Flintridge, and Riverside in southern California. We expect the number of bee species collected in these cities to increase as sampling continues in 2009 and beyond. More than 1,600 species are known from the entire state.

ACKNOWLEDGEMENTS

We thank the California Agricultural Experiment Station for major support of this research. Ann Campbell of Ukiah, California generously allowed us the opportunity to study and monitor bees and plants in her garden. She also permitted us to add several plant types to the garden that are known to attract native bee species. Misha Leong kindly read an early draft of the paper.

We dedicate this paper to Roy Snelling – a good friend and fellow bee biologist. Roy was always willing to help us with new and interesting bee taxonomic and behavioral/ecological problems. His enthusiastic and generous personality will be sorely missed.

Table 3. Native and non-native plant species attracting highest numbers of bee taxa in Ukiah garden, 2005–2008.

Plant species	Nos. of attracted bee taxa: Genera	Nos. of attracted bee taxa: Species	Flower Months
Natives			
Carpenteria californica Torr.	9	15	5
Solidago californica Nutt.	9	15	7 to 9
Erigeron glaucus Ker Gawl.[2]	9	12	5 to 10
Achillea millefolium L.	6	7	5,6,8,9
Grindelia hirsutula Hook. & Arn.[3]	4	4	5 to 8
Non-Natives			
Nepeta × *faassenii* Bergmans	14	28	5 to 10
Perovskia atriplicifolia Benth.	8	18	6 to 10
Lavandula sp. 2	11	17	6 to 8
Erigeron karvinskianus DC.	11	17	4 to 10
Aster × *frikartii*[3]	6	10	7 to 9

[1] Plants listed in decreasing order of diverse bee species.
[2] Mostly from added *E. glaucus* 'Wayne Roderick'
[3] Added plant species to garden - not previously in garden.

LITERATURE CITED

Ahrne, K., J. Bengtsson, and T. Elmqvist. 2009. Bumble bees (*Bombus* spp.) along a gradient of increasing Uubanization. *PLoS ONE* 4 (5): e5574 Available at www.plosone.org. Accessed 26 May 2009.

Antonini, Y. and R. P. Martins. 2003. The flowering-visiting bees at the ecological station of the Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil. *Neotropical Entomology* 32: 565–575.

Brenzel, K. N. ed. 2007. *Sunset Western Garden Book.* Sunset Publ. Corp., Menlo Park, California. 768 pp.

Cane, J. H. 2005. Bees, pollination, and the challenges of sprawl. Pp. 109–124 *in*: Johnson, E. A. and M. W. Klemens. eds. *Nature in Fragments: the Legacy of Sprawl.* Columbia Univ. Press, New York, N.Y. 400 pp.

Carroll, S. B. and S. D. Salt. 2004. *Ecology for Gardeners*. Timber Press. Portland, OR. 328 pp.

Fetridge, E. D., J. S. Ascher, and G. A. Langellotto. 2008. The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Annals of the Entomological Society of America* 101: 1067–1077.

Frankie, G. W., R. W. Thorp, M. Schindler, J. Hernandez, B. Ertter, and M. Rizzardi. 2005. Ecological patterns of bees and Their host ornamental flowers in two northern California cities. *Journal of the Kansas Entomological Society* 78: 227–246.

———, R. Thorp, J. Hernandez, M. Rizzardi, B. Ertter, J. C. Pawelek, S. L. Witt, M. Schindler, R. Coville, and V. Wojcik. 2009. Native bees are a rich natural resource in urban California gardens. *California Agriculture* 63: 113–120.

Grissell, E. 2001. *Insects and Gardens*. Timber Press, Portland, Oregon. 345 pp.

Hayes, A. 2003. Gardening for wildlife with native plants. *Bay Nature* 3: 17, 31–32.

Hernandez, J. 2009a. Bee visitation (Hymenoptera: Apoidea) in a newly constructed urban garden in Berkeley, California. *Apidologie*. Submitted, in review.

———, G. W. Frankie, and R. W. Thorp. 2009b. Ecology of Urban Bees: A review of current knowledge and directions for future study. *Cities and the Environment*. Submitted, in review.

Hickman, J. C. ed. 1993 *The Jepson Manual of Higher Plants of California*. University of California Press, Berkeley, California. 1400 pp.

Louv, R. 2008. *Last Child in the Woods: Saving Our Children from Nature-Deficit Disorder*. Algonquin Books, Workman Publishing, NY, New York. 391 pp.

Lowry, J. L. 1999. *Gardening with a Wild Heart*. University of California Press, Berkeley, CA. 253 pp.

———. 2007. *The Landscaping Ideas of Jays*. The University of California Press, Berkeley, California. 281 pp.

Owen, J. 1991. *The Ecology of a Garden: The First Fifteen Years*. Cambridge University Press, Cambridge. 403 pp.

Pawelek, J. C., G. W. Frankie, R. W. Thorp, and M. Przybylski. 2009. Modification of a community garden to attract native bee pollinators in urban San Luis Obispo, California. *Cities and the Environment* (in press).

National Research Council (NRC). 2007, *Status of Pollinators in North America*. The National Academies Press, Washington, D.C. 307 pp.

Stearns, P. W. 2007. *A Journey in Time: Mendocino County Wildflowers*. Peter W. Stearns Enterprises, Ukiah, CA. 198 pp.

Stone, M. K. and Z. Barlow, eds. 2005. *Ecological Literacy*. Sierra Club Books, San Francisco, CA. 275 pp.

Tallamy, D. W. 2009. *Bringing Nature Home*. Timber Press, Portland, Oregon. 358 pp.

Wojcik, V. A., G. W. Frankie, R. W. Thorp, and J. Hernandez. 2008. Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *Journal of the Kansas Entomological Society* 81: 15–28.

J. HYM. RES.
Vol. 18(2), 2009, p. 380

Thank you

GORDON C. SNELLING

13161 Rancherias Road, Apple Valley, CA 92308, USA;
email: myrmecophile@armyants.org

I would like to thank the editors, publishers and authors who contributed their time and talent to this project, to all of you, thank you.

There is no doubt that Roy would think we are all silly (although I suspect his terminology would be a bit stronger) for doing this in his honor, however the way I see it is he is not here to complain so we're doing it anyway. Not only can he not complain but it's a good way to get some valuable papers out there and say farewell to a valued colleague, friend and parent.

The sad truth is that the odds are good that many of you knew him better than I ever did so I want to thank you for the insights and stories that have been shared with me, both here and personally. Thank you all.

INSTRUCTIONS FOR AUTHORS

General Policy. *The Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are acceptable if the species has economic importance or provides new data on the biology or evolution of the genus or higher taxon. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level. All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript. The language of publication is English. Summaries in other languages are acceptable. This journal is ISI-listed.

The deadline for receipt of manuscripts is 1 September (for the April issue) and 1 March (for the October issue).

Format and Preparation. Authors are strongly encouraged to submit manuscripts electronically to the editor at the email address below, and in the format specified below. On the upper left of the title page give name, address, telephone and fax numbers, and email address of the author to whom all correspondence is to be sent. The paper should have a concise and informative title, followed by the names and addresses of all authors. The sequence of material should be: title, author(s), abstract, text, acknowledgments, literature cited, appendix, figure legends, figure copies (each numbered and identified), tables (each numbered and with heading). Each of the following should start a new page: (1) title page, (2) abstract, (3) text, (4) literature cited, (5) figure legends, (6) footnotes.

Upon **final acceptance** of a manuscript, the author should provide the editor with an emailed IBM formatted electronic version. CD-ROMs or 3.5 inch floppy disks are acceptable. Because symbols and tables are not always correctly translated it is best to also send a printed copy of the manuscript. Preferred word processing programs are Microsoft Word and WordPerfect. If possible, all words that must be italicized should be done so, not underscored. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double-spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. CDs and Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

Illustrations should be planned for reduction to the dimension of the printed page (14 × 20.5 cm, column width 6.7 mm) and allow room for legends at the top and bottom. Do not make plates larger than 14 × 18 in. (35.5 × 46 cm). Individual figures should be mounted on a suitable drawing board or similar heavy stock. Photographs should be trimmed, grouped together and abutted when mounted. Figure numbers should be on the plate. Include title, author(s) and address(es), and illustration numbers on back of each plate. Original figures need not be sent until requested by the editor, usually after the manuscript has been accepted. Reference to figures/tables in the text should be in the style "(Fig.1)" "(Table 1)". Measurements should be in the metric system.

Electronic plates may be submitted on disc, via email or uploaded to an ftp site (instructions will be given). They must be fully composited, labeled, and sized to fit the proportions of the journal page. Line art should be scanned at 1200 dpi (minimum input resolution is 600 dpi). Color or grayscale (halftone) images should have a dpi of 300-350. Color files should be in CMYK and not RGB. Graphics should be submitted as TIFF, Adobe Illustrator or EPS files. No PowerPoint or Word/WordPerfect files with images embedded in them are acceptable.

All papers must conform to the *International Code of Zoological Nomenclature*. The first mention of a plant or animal name should include the full scientific name including the authority. Genus names should not be abbreviated at the beginning of a sentence. In taxonomic papers type specimens must be clearly designated, type depositories must be clearly indicated, and new taxa must be clearly differentiated from existing taxa by means of keys or differential diagnoses. Authors are required to deposit all type material in recognized institutions (not private collections). Voucher specimens should be designated for specimens used in behavioral or autecological studies, and they should be deposited similarly. DNA sequences must be deposited in GenBank/EMBL/DNA Databank of Japan.

Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used, including discussion of program options used. A data matrix should be provided for morphological characters. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and reasons given for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

Charges. Publication charges are $10.00 per printed page. At least one author of the paper must be a member of the International Society of Hymenopterists. Reprints are charged to the author and must be ordered when returning the proofs; there are no free reprints. Author's corrections and changes in proof are also charged to the author. Color plates will be billed at full cost to the author.

All manuscripts and correspondence should be addressed to:

Dr Gavin Broad
Dept. of Entomology
The Natural History Museum
Cromwell Road
London SW7 5BD, UK
Phone: +44(0)207 9425938; Fax: +44(0)207 9425229; Email: editor@hymenopterists.org

CONTENTS
(Continued from front cover)